SBM 1020

BRITISH MUSEU
(NATURAL HISTORY)
30 MAR 1988
PRESENTED
GENERAL LIBRAR

Bulletin of the British Museum (Natural History)

Cenomanian and Lower Turonian echinoderms from Wilmington, south-east Devon, England

A. B. Smith, C. R. C. Paul, A. S. Gale &
S. K. Donovan

Geology series Vol 42 31 March 1988

SHOUT
SHARE
IT

The *Bulletin of the British Museum (Natural History)*, instituted in 1949, is issued in four scientific series, Botany, Entomology, Geology (incorporating Mineralogy) and Zoology, and an Historical series.

Papers in the *Bulletin* are primarily the results of research carried out on the unique and ever-growing collections of the Museum, both by the scientific staff of the Museum and by specialists from elsewhere who make use of the Museum's resources. Many of the papers are works of reference that will remain indispensable for years to come.

Parts are published at irregular intervals as they become ready, each is complete in itself, available separately, and individually priced. Volumes contain about 300 pages and several volumes may appear within a calendar year. Subscriptions may be placed for one or more of the series on either an Annual or Per Volume basis. Prices vary according to the contents of the individual parts. Orders and enquiries should be sent to:

Publications Sales,
British Museum (Natural History),
Cromwell Road,
London SW7 5BD,
England.

BRITISH MUSEUM
PUBLICATIONS
ISSUED
31 MAR 1988
SALES OFFICE
NATURAL HISTORY

World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Geol.)

Erratum

Bulletin British Museum (Natural History)
Geology Volume **42**, March 1988

Smith, Paul, Gale and Donovan

Cenomanian and Lower Turonian echinoderms from Wilmington, south-east Devon, England.

Please note that Plates 11 and 12 have been transposed in error.

BRITISH MUSEUM
(NATURAL HISTORY)
30 MAR 1988
PRESENTED
GENERAL LIBRARY

Cenomanian and Lower Turonian echinoderms from Wilmington, south-east Devon, England

A. B. Smith

Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD

C. R. C. Paul

Department of Geology, Liverpool University, Liverpool L69 3BX

A. S. Gale

Department of Geology, City of London Polytechnic, Walburgh House, Bigland Street, London E1 2NG

S. K. Donovan

Department of Geology, University of the West Indies, Mona, Kingston 7, Jamaica

Contents

Synopsis 1
Introduction 2
Lithostratigraphy 4
Biostratigraphy 11
Echinoids. By A. B. Smith 16
  Introduction 16
  Faunal changes and echinoid palaeoecology 17
    Modes of life 20
    Palaeoecological analysis of species distribution 25
  Predation and parasitism 30
  Evolutionary changes 31
  Systematic descriptions 35
  Species composition and abundance in units a to j 183
Asteroids. By A. S. Gale 189
  Introduction 189
  Systematic descriptions 192
Crinoids. By C. R. C. Paul and S. K. Donovan 208
  Introduction 208
    Palaeoecology and preservation 210
    Pathological anomalies 211
    Stratigraphical distribution 211
    Evolutionary changes 213
  Systematic descriptions 213
Acknowledgements 235
References 235
Systematic Index 241

Synopsis

The echinoderm fauna from a working quarry at Wilmington, SE Devon, is both abundant and diverse, with 36 species of echinoid, 18 of asteroid and 7 of crinoid that are described here. Sediments ranging from coarse sands to pure chalk are exposed, in beds ranging from basal Lower Cenomanian to Lower

Bull. Br. Mus. nat. Hist. (Geol.) **42** : 1–245

31 March 1988

Turonian. Almost 2300 specimens have been collected and their stratigraphical horizon recorded within the section. The succession is correlated, using Shaw's quantitative method, with the better-known coastal section at Beer, south Devon, where rates of sedimentation can be shown to differ.

Ten of the echinoid species have not previously been reported from Britain although they are known from elsewhere. The most probable life style of each is deduced from functional analysis, and the changing abundances of individual echinoid species is interpreted in palaeoecological terms. Amongst irregular echinoids there are epipsammic grazers, bulk sediment swallowers and selective deposit feeders, some using phyllode tube feet, others their frontal ambulacrum to collect sediment. Echinoids with different feeding strategies dominate at different stratigraphical levels. Rare specimens show evidence of gastropod and fish predation, while about 2% of the population of some regular echinoid species show parasite-induced growth abnormalities, some produced by endoparasitic infestation of a gonad, others by ectoparasitic boring gastropods. Although most species remain morphologically static throughout their range, *Discoides subuculus* shows ecophenotypic variation related to sediment grain size and *Echinogalerus rostratus* progressive gradual evolution towards a more rostrate test and a smaller peristome.

Asteroids occur only as isolated ossicles but show that a highly diverse fauna existed. Only a proportion can be ascribed to species or even genus without more complete material. The fauna is dominated by species of Goniasteridae (12 of the 18 species).

Crinoids form a minor element of the fauna although isolated columnals and fragments of stem are not uncommon. One new species, *?Isocrinus undulatus*, is described. Crinoids are most common where echinoids are rarest and appear to have been adapted to life on semi-mobile substrates in moderate current regimes.

Lectotypes for *Diadema benettiae* Forbes (= *D. ornatum* Woodward, *non* Goldfuss), *Polydiadema bonei* (Woodward) and *Phocidaster grandis* Spencer are selected. The diagnosis of *Labrotaxis tricarinata* (Lambert) is amended.

Introduction

A large working quarry known as the White Hart sand pit lies on the outskirts of the village of Wilmington, some two miles east of Honiton, Devon (National Grid reference SY 208999). Here a thick and highly fossiliferous sequence of Upper Cretaceous sands and chalk can be examined. A large part of the succession is Lower Cenomanian in age but there are thin Middle and Upper Cenomanian deposits as well as several metres of Lower Turonian chalk. The Cenomanian sands have been quarried here for approximately 150 years and were first mentioned by Fitton (1836).

This is a small outlier of Upper Cretaceous preserved by local downfaulting which lies at the most westerly point of Upper Cretaceous outcrop in Britain (Fig. 1). Here the Cenomanian is represented by sand facies whereas to the east of Dorset the same horizons are in chalk facies. The quarry yields a remarkably abundant and diverse fauna, over 300 species being recorded (MacFayden 1970), many of them found nowhere else in Britain. The fauna resembles that from the type Cenomanian of the Sarthe district, western France. Despite the importance of this quarry both geographically and faunally, few studies on the lithology or fauna of the Wilmington outlier have been published. The beds were first investigated by Jukes-Browne (1898) and Jukes-Browne & Hill (1903), while Smith (1957*a*, *b*, 1961), Hancock (1969) and Kennedy (1970) have all added to our knowledge.

This project was begun in 1981 as a microstratigraphical investigation of echinoderm distribution within the highly fossiliferous sequence at Wilmington. Over 50 species of echinoderms occur in the White Hart sand pit and we wished to investigate problems of sampling efficiency, quantitative biostratigraphical correlation, ecological niche separation and the mode and tempo of evolution. What sample size was necessary to get an adequate representation of the fauna and how efficient was our sampling at different levels? How are species distributed within the section? Can species associations be recognized and how is ecological space partitioned between coexisting species? How much of the faunal succession reflects evolutionary change and how much ecological replacement? What appear to be the principal factors in bringing about ecological replacement? Can evolutionary change be recognized and, if so, is it gradual or rapid? How does the faunal succession at Wilmington match that seen elsewhere,

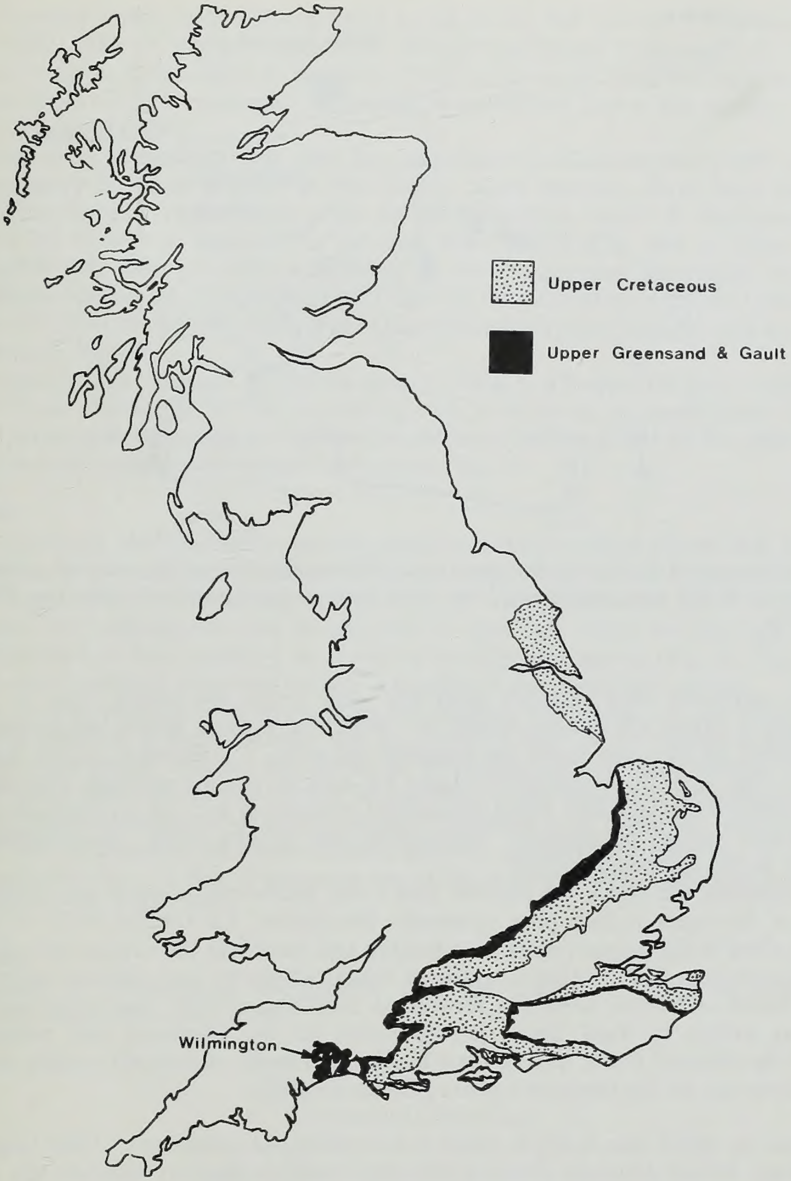


Fig. 1 Outcrop map of Cretaceous rocks in Britain showing the location of Wilmington.

particularly at the nearby coastal section of south-eastern Devon, and could a quantitative biostratigraphical approach lead to a much more refined biostratigraphy?

To attempt to answer some of these questions, the microstratigraphical distribution of the echinoderm fauna at the White Hart sand pit was studied. All echinoderm material, whole or fragmentary, located *in situ* was collected and the stratigraphical position of each specimen was recorded in cm from a reference datum level. Some 2000 specimens were collected in this way, almost 1500 of which were identifiable echinoids, nearly 100 were asteroid ossicles and 136 were identifiable crinoid pieces: the remainder were indeterminate echinoid or echinoderm frag-

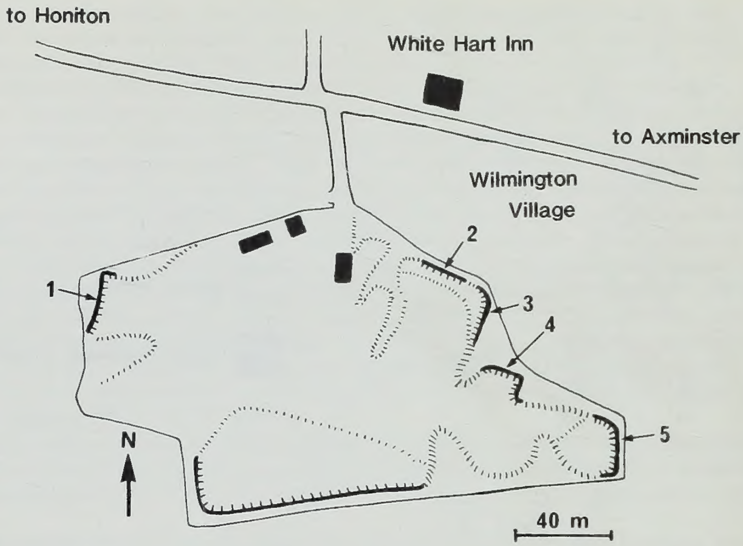


Fig. 2 Sketch map of the White Hart sand pit at Wilmington, Devon, showing the position of the five faces (1–5) that were logged and from which accurate stratigraphical collections of the fauna were made.

ments. The specimens were collected from five faces within the quarry (Fig. 2). Because of lateral variation within the quarry, caused by differential erosion before the deposition of the Turonian chalk, no one face shows the complete sequence. A composite section was therefore constructed (Fig. 4, p. 8). A correction factor for each of the five sections was calculated to make the datum levels identical, using lithological correlation and the distribution of the three most abundant species of echinoid. Throughout the present work, stratigraphical heights always refer to this composite section.

Having collected the fauna, we realized that a full taxonomic revision was essential, and a large part of this work is thus pure systematic description. All authors were at one time or another involved in the primary work of collecting and recording the stratigraphical position of the fauna accurately. The detailed analysis of lithostratigraphy and sedimentology was done jointly by Smith and Paul, while the section on biostratigraphical correlation and sampling analysis was written by Paul. Smith is responsible for the taxonomy and palaeoecological analysis of the echinoid fauna (p. 16), Gale for the taxonomy of asteroid ossicles (p. 189), and Paul and Donovan for the taxonomy of the crinoids (p. 208).

The material on which this study is based is housed in the collections of the Department of Palaeontology, British Museum (Natural History), London. Register numbers are prefixed by E. Other material is in the British Geological Survey collections, register numbers prefixed GSM.

Lithostratigraphy

Introduction

The Wilmington Inlier is about the most westerly outcrop of Cenomanian in Britain and lies to the west of the 'mid-Dorset swell', a topographical high that divided southern England into two basins during the Cenomanian (see Drummond 1970, Kennedy 1970). To the west of this swell, chalk sedimentation was relatively late in appearance and much of the Cenomanian is represented by a condensed sequence of sands and sandy limestones, unlike the equivalent beds of south-east England where chalk sedimentation began during the Lower Cenomanian. The first worker to realize that the highest fossiliferous beds of the 'Upper Greensand' of Devon were Cenomanian in age and equivalent to the Grey Chalk of south-east England was Jukes-Browne (1898). A summary of the Cenomanian succession in south-east Devon has recently been given by Jarvis & Woodruff (1984).

The succession at Wilmington was also first described by Jukes-Browne (1898) and a fuller account was given in Jukes-Browne & Hill (1903). More recently, there have been several accounts of the detailed stratigraphy given by Smith (1957*a*), Smith & Drummond (1962), Kennedy (1970), Wright & Kennedy (1981) and Hart (1983). The best of these is that of Kennedy (1970) who also provided a zonation of the Wilmington succession based on the ammonite fauna (see Fig. 4). This showed that most of the succession is Lower Cenomanian in age and that much of the Middle and Upper Cenomanian is absent through erosion or present only as a remanié deposit.

There is considerable variation within the quarry owing to a major erosional surface beneath the Middle Chalk which cuts out the underlying beds to a greater or lesser extent. The Lower to Middle Cenomanian deposits are thickest in the most northern face of the quarry and are most deeply eroded in the western face of the quarry (Fig. 3).

Field method

As already explained, the succession was examined and fauna collected from five faces within the quarry (Fig. 2). At each face the major erosional surface was used as a datum level and the succession logged (Fig. 3). The stratigraphical level at which individual fossils were collected was measured with reference to the datum level at that face. Since no one face shows the complete succession, it was necessary to construct a composite section (Fig. 4). The heights at which fossils were collected were then corrected to refer to this composite section.

Sediment samples were taken at 50 cm intervals or closer from faces 1, 4 and 5, and again the stratigraphical position of these samples was corrected to refer to the standard section. Most bulk samples were poorly lithified and could be disaggregated with little trouble: these were analysed for grain size and sorting by dry sieving. Hard, well-cemented limestones were thin-sectioned and point-counted and samples were also dissolved in HCl and the residue dry sieved for analysis. For all samples the mean, median, graphic standard deviation (d_G or d_I) and the skewness coefficient (Sk_G or Sk_I) of the grain size of the sediment were calculated following the procedures set out by Folk (1968).

The succession

The succession at Wilmington is divisible into the following seven lithological units (nomenclature follows Kennedy, 1970):

7. Middle Chalk
6. Bed C
5. Wilmington Limestone
4. Grizzle
3. Wilmington Sands
2. Basement Bed
1. 'Upper Greensand'

1. 'UPPER GREENSAND'. In the deepest part of the quarry, the south-east corner, some 2 m of coarse, poorly sorted greensand are exposed. The lowest beds visible are coarse, glauconite-rich sands with a median grain size of 1·85 Ø, a mean grain size of 2·53 Ø, d_G 2·12 and Sk_G 0·48. Occasional thin lenses of red clay are present at this level. Higher up, the sediment becomes rather better cemented and by 1068 cm below standard datum the rock is a coarse sandy limestone. Calcitic grains form 61% of the sand fraction whereas quartz grains amount to only 17% (the remainder being either glauconite or recognizable fossil debris). A small amount of chalky matrix is present but forms less than 3% of the whole rock. Sparry calcite fills most of the pore space.

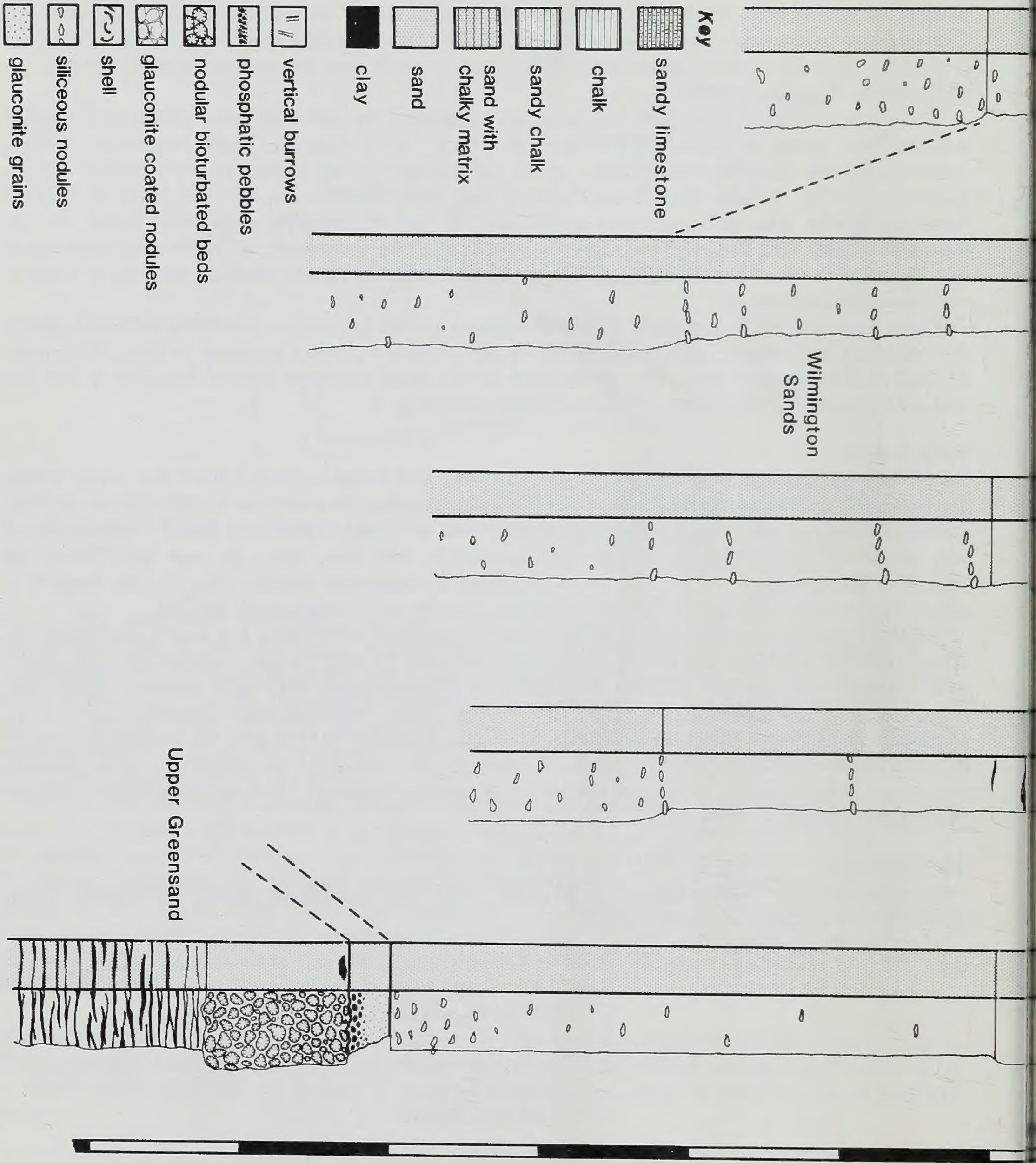
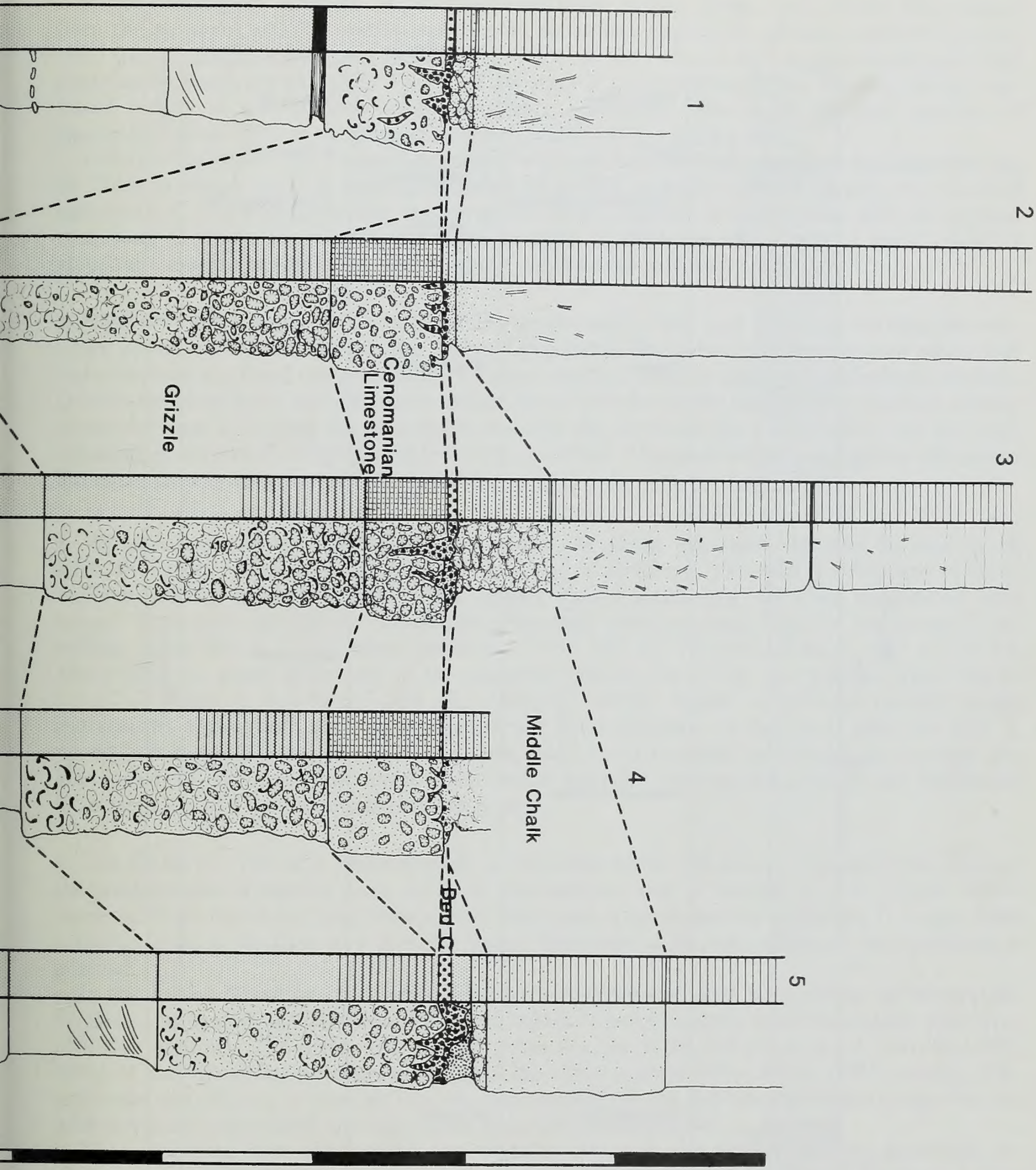

Key
sandy limestone
chalk
sandy chalk
sand with chalky matrix
sand
clay
vertical burrows
phosphatic pebbles
nodular bioturbated beds
glauconite coated nodules
shell
siliceous nodules
glauconite grains
Wilmington Sands
Upper Greensand

Fig. 3 Detailed sedimentary logs and lithological correlation of the five faces


1
2
3
4
5
Grizzle
Cenomanian Limestone
Middle Chalk
Bed C

Wilmington White Hart sand pit from which collections were made (see Fig. 2, p. 4).

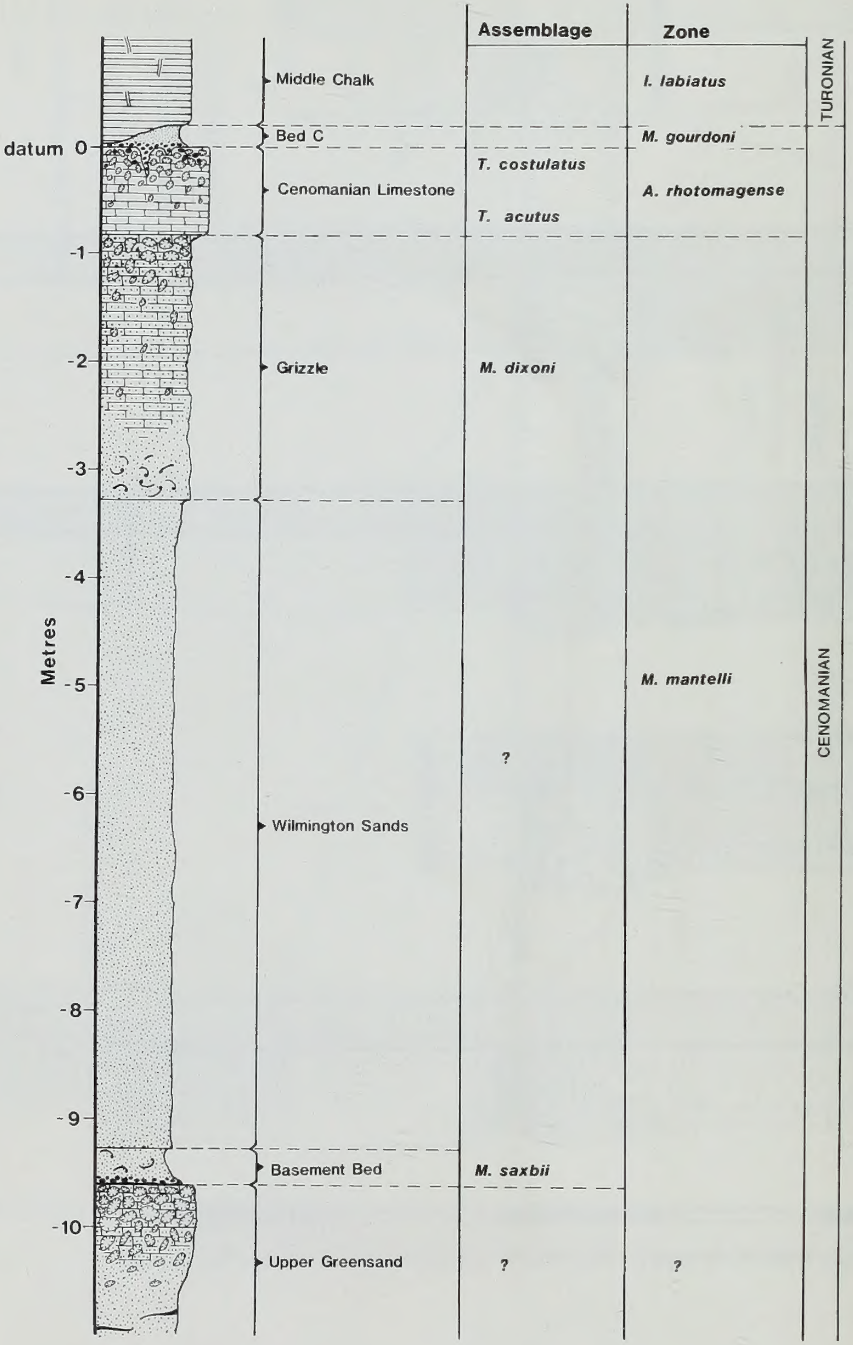

Assemblage
Zone
Middle Chalk
I. labiatus
TURONIAN
datum 0
Bed C
M. gourdoni
Cenomanian Limestone
T. costulatus
A. rhotomagense
T. acutus
-1
-2
Grizzle
M. dixoni
-3
-4
Metres
-5
M. mantelli
CENOMANIAN
?
-6
Wilmington Sands
-7
-8
-9
Basement Bed
M. saxbii
-10
Upper Greensand
?
?

Fig. 4 Composite section for the succession exposed at Wilmington. Ammonite zonation is taken from Kennedy (1970).

Slightly higher, at 1018 cm below standard datum, calcite grains have almost disappeared from the sediment and the matrix has become noticeably chalky. In addition, scattered gravel-sized quartz grains have appeared, forming 4–5% of the rock, as well as the occasional small glauconite-coated nodule. Only 18·5% of the rock is non-carbonate, this fraction being composed largely of quartz grains with subsidiary glauconite. The matrix includes patches of sparite but about 70% of the interstitial space is filled with a chalky marl.

Towards the top of the 'Upper Greensand' the beds become highly nodular, with nodules up to 15 cm in length set in a green glauconitic clay. This nodularity is presumably the result of bioturbation. The non-carbonate residue at this level is again low, only about 20% of the total rock, and, as below, the matrix within the nodules is predominantly chalky. A thick veneer of glauconite marks the top of this bed at about 945 cm below standard datum.

2. **Basement Bed.** Some 20–23 cm of muddy quartz sands, finer and better sorted than the beds either above or beneath, overlies the 'Upper Greensand'. Bivalves are fairly common within this bed and there is a basal concentration of rather small (centimetre diameter) phosphatic nodules. Occasional phosphatic nodules occur within the lower part of the bed but they become smaller above the base. Excluding the phosphatic nodules, the sediment has a mean grain size of 1·5 ∅, a median grain size of 2·0 ∅, Sk_I of 0·39 and d_I of 0·41. The great majority of grains are quartz but some glauconite grains are also present.

3. **Wilmington Sands.** The Wilmington Sands are about 6 m thick and can be seen in all faces, though the basal part can only be examined in section 5. This unit is composed of fairly uniform, poorly bedded, yellow-brown, friable quartz sands that are only moderately well sorted. The sands are slightly coarser and less well sorted at their base. In the lowest 2 m, median grain size is 1·3 ∅, mean grain size 1·1–1·2 ∅, d_I 1·2–1·4 and Sk_I −0·07 to +0·11. Above this the mean grain size of the sediment falls to 1·4–1·6 ∅, the median grain size to 1·5–1·7 ∅ while d_I is 0·99–1·2 and Sk_I −0·22 to +0·04. Bands of siliceous nodules occur sporadically throughout the succession but are more common in the lower part (see Fig. 3, pp. 6–7). Between 4·5 and 5·5 m below datum, small pyrite nodules, up to 5 mm in diameter, are also found. In the uppermost metre or so, rather irregular iron-stained partings are found and in sections 1 and 5 distinct cross-bedding is seen.

4. **The Grizzle.** This unit varies slightly in thickness within the quarry, ranging from 2·6 m at the western end of section 2, to 2·1 m at the southern end of section 3. It is slightly better cemented than the underlying Wilmington Sands and is much more fossiliferous. It ranges from a chalky sand at its base to a nodular sandy limestone at its top, although the transition is gradual.

In the lowest 50 cm or so a weak nodularity is developed and large valves of inoceramid bivalves and oysters are common. The sand, which is poorly sorted, is a little coarser than that of higher samples. The mean and median grain size are both 1·45 ∅, d_I is 1·41 and Sk_I 0·07. Most of the interstitial pore space is empty but there is some 10% of fine chalky matrix. The grain-size distribution is more or less the same as that for the Wilmington Sands except for the addition of an appreciable amount of silt- and mud-sized particles.

The succeeding beds are initially less nodular although the very occasional glauconite or phosphate-coated pebble can be found (the lowest coated intraclast was found at 282 cm below datum). There is a relative decrease in the amount of quartz grains and an increase in the amount of fine chalky matrix up the succession. Quartz grains form about 80% of the rock at 325 cm below standard datum level, but only 40–45% at 275 and 225 cm below standard datum and 38% at 160 cm below standard datum. There is a corresponding increase in the quantity of chalky matrix and carbonate and so, by the top of the Grizzle, chalky matrix has increased from about 10% to 35% of the rock. Nodularity of the beds also becomes more pronounced up the succession and towards the top glauconite-draped nodules together with the occasional phosphatic nodule become abundant.

5. The Wilmington Limestone. A durable, well-lithified limestone overlies the Grizzle, but is only preserved in the middle part of the quarry (sections 2, 3 and 4). Eastwards and westwards it has been removed by erosion before the deposition of Bed C. Following the Wilmington Limestone eastwards from face 4 to face 5 it changes from a solid limestone 50 cm thick to a thinner creviced and occasionally undercut limestone, and then to loose, isolated blocks more or less surrounded by Bed C; before finally disappearing.

The limestone has only 8–18% non-carbonate content (mostly quartz grains) and 50–60% fine chalky matrix. Patches of sparry calcite occur scattered throughout. The sand fraction of this limestone is poorly sorted. In the upper 30–40 cm, glauconite- and phosphate-coated nodules become abundant and towards the top they form a pebble conglomerate. The Wilmington Limestone is at its thickest in section 2 where it reaches a thickness of 80 cm. Crevicing and some large burrow systems carry glauconitic sand and phosphatic pebbles of Bed C far down into the Wilmington Limestone.

6. Bed C. This is a fairly well-sorted glauconite sand 20–23 cm thick in section 5 but thinning to almost nothing westwards, where it is represented by a thin veneer capping the Wilmington Limestone and infilling surface fissures. Phosphate-coated nodules, ranging from a few mm to one or two cm in diameter, form a pebble conglomerate at the base of this bed, but unlike the nodular top of the Wilmington Limestone these nodules are unlithified. The sands are a strong green colour and are composed of medium- to fine-grained glauconite grains together with some quartz grains. Whole-rock analysis of the pebble conglomerate gave a median and mean grain size of 0·4 $\varnothing$, d_I as 2·18 and Sk_I as 0·23.

Above the basal phosphatic pebble bed there is an almost pure, dark-green glauconite sand. This is moderately well sorted and lacks any appreciable clay- or silt-sized particles. The mean and median grain size are 1·6 $\varnothing$, d_I is 1·05 and Sk_I is 0·05. No fossil shell material occurs in this glauconite sand and the echinoids collected from it were all phosphatized and formed pebbles in the pebble conglomerate.

7. Middle Chalk. The phosphatic layer of Bed C is overlain in sections 1, 2 and 3 by a 20–30 cm bed of green-speckled sandy chalk, strongly bioturbated. Quartz and glauconite grains form up to 10% of the rock, the remainder being chalk. Above this, quartz grains disappear and glauconite becomes progressively rarer until finally lost. A few large semi-vertical and parallel-sided burrows occur scattered within the lowest 2–3 m of chalk, but generally the bedding is undisrupted and there is little shell material present. At least 6 m of chalk can be examined in section 1.

Sedimentary history

The sequence at Wilmington is entirely marine and consists of four phases of net sediment influx separated by glauconitic and phosphatic pebble beds. The 'Upper Greensand' was initially a coarse, poorly-sorted, permeable quartz sand but the influx of quartz grains became drastically curtailed and the sediment became a calcarenite. Towards the top of the 'Upper Greensand' the sands became progressively more muddy. Following a marked hiatus in sedimentation, during which phosphate-coated pebbles were formed, the next phase of deposition began with a coarse shelly lag deposit, the Basement Bed, and continued uninterrupted right through to the top of the Grizzle. Initially, sedimentation was probably rapid and little mud was deposited. The sands must have been loose and unconsolidated and the sea floor was occasionally rippled. In the Grizzle, the influx of quartz sand began to be diluted by carbonate mud, possibly as the rate of sedimentation slowed. By the top of the Grizzle, the input of sediment had become slow enough for lithified intraclasts to be formed. This phase of sedimentation ended with another lightly-phosphatized and glauconitic pebble bed.

The Wilmington Limestone represents a third and much briefer pulse of sedimentation. Once again the sediment was less muddy at the onset of deposition and became muddier towards the top before another phosphatic nodular bed was developed marking a third hiatus in sedimentation. There then followed a major erosional phase during which the Cenomanian Limestone was partly removed. Finally, after a pulse of glauconitic sand was swept across the area, chalk sedimentation commenced and the small amount of quartz sand still being brought in rapidly disappeared.

Comparison with previous work

Presumably because of the lateral variation that exists within the pit, earlier descriptions of the lithostratigraphy at Wilmington sometimes differ considerably from the account given here. Smith (1957a, b) gave a reasonable account of the succession but with very much smaller thicknesses for the Limestone and Grizzle. His account of the quarry was copied by MacFadyen (1970). Kennedy (1970) gave a detailed account of the succession that is more or less identical with ours, although the lowest beds were not exposed at that time. Wright & Kennedy (1981: text-fig. 5) published a log of part of the succession from the top of the Wilmington Limestone to the base of the Middle Chalk. They described two glauconitic hard grounds, between which there was 140 cm of Bed C composed of an upper 80 cm of hard, splintery quartzose chalk and a lower 60 cm of soft quartzose glauconitic chalk (seen at the western end of the White Hart sand pit, but no evidence of this now remains). Finally, Hart (1983) provided a sedimentary log of the entire sequence and was able to reach stratigraphically lower levels than we have observed. There are two minor discrepancies between his section and our lithostratigraphical logs. Firstly he found the distance between the pebble bed at the top of the 'Upper Greensand' and the top of the Wilmington Limestone to be somewhat over 12 m, whereas we measured it as 9·45 m in section 5. Secondly, Hart indicates three levels of nodularity, with about $1\frac{1}{2}$ m of nodularity developed some 5–6 m below the top of the Wilmington Limestone: we found no evidence of this.

Biostratigraphy

Correlation

The correlation of the sections at Wilmington has been discussed by Kennedy (1970: 664), Wright & Kennedy (1981: 13, 1984: 14) with respect to ammonite zonation, and Carter & Hart (1977: 100) on foraminifera. Our summary of the conventional ammonite zonation is given in Fig. 4, p. 8. On the basis of a rather meagre microfauna, Carter & Hart (1977: 100) suggested that the base of the Wilmington Sands was in their foraminiferal Zone 10 and the Grizzle in Zone 11a, but they were unable to suggest the position of the boundary in between. Neither previous zonal scheme relied on echinoderms and, so far, we have been unable to confirm any zonal boundaries. Here we present a graphic correlation (Shaw 1964) with the section along the coast between Beer and Branscombe.

We do not propose to erect a new zonal scheme based on echinoderms. Nor will we refer occurrences of echinoderms to previously defined zones even if that were possible, because recording occurrences of fossils to the nearest zone is unsatisfactory for three reasons (see Shaw 1971, Hay 1974 for a discussion.) Firstly, it automatically increases apparent stratigraphical range, down to and up to the nearest zonal boundaries, below and above the real first and last known occurrences. Extensions of ranges are often dramatic in short-lived species, but are present even in long-ranging species (Paul 1985: 13). Secondly, it obscures the sequence of appearances and disappearances, crowding them together at zonal boundaries, whereas it is this sequence which is the key to accurate correlation. Finally, probably most important, it defines the accuracy of correlation (to the nearest zone) at the outset and refinement of correlation is impossible no matter how much additional collecting and recording is undertaken. Quantitative correlation techniques are potentially far more accurate than correlation using zones. Blank & Ellis (1982) and Sweet (1984), using two different methods, improved the accuracy of correlation by at least an order of magnitude. All quantitative methods depend on accurately known ranges of fossils recorded in measured sections or logged borehole cores (Shaw 1971, Hay 1972, 1974, Harper 1981, Paul 1985). The first point that needs to be settled, then, is how adequate our sampling has been. Just how well do we know the ranges of the echinoderms at Wilmington? The question can best be answered with a specific example.

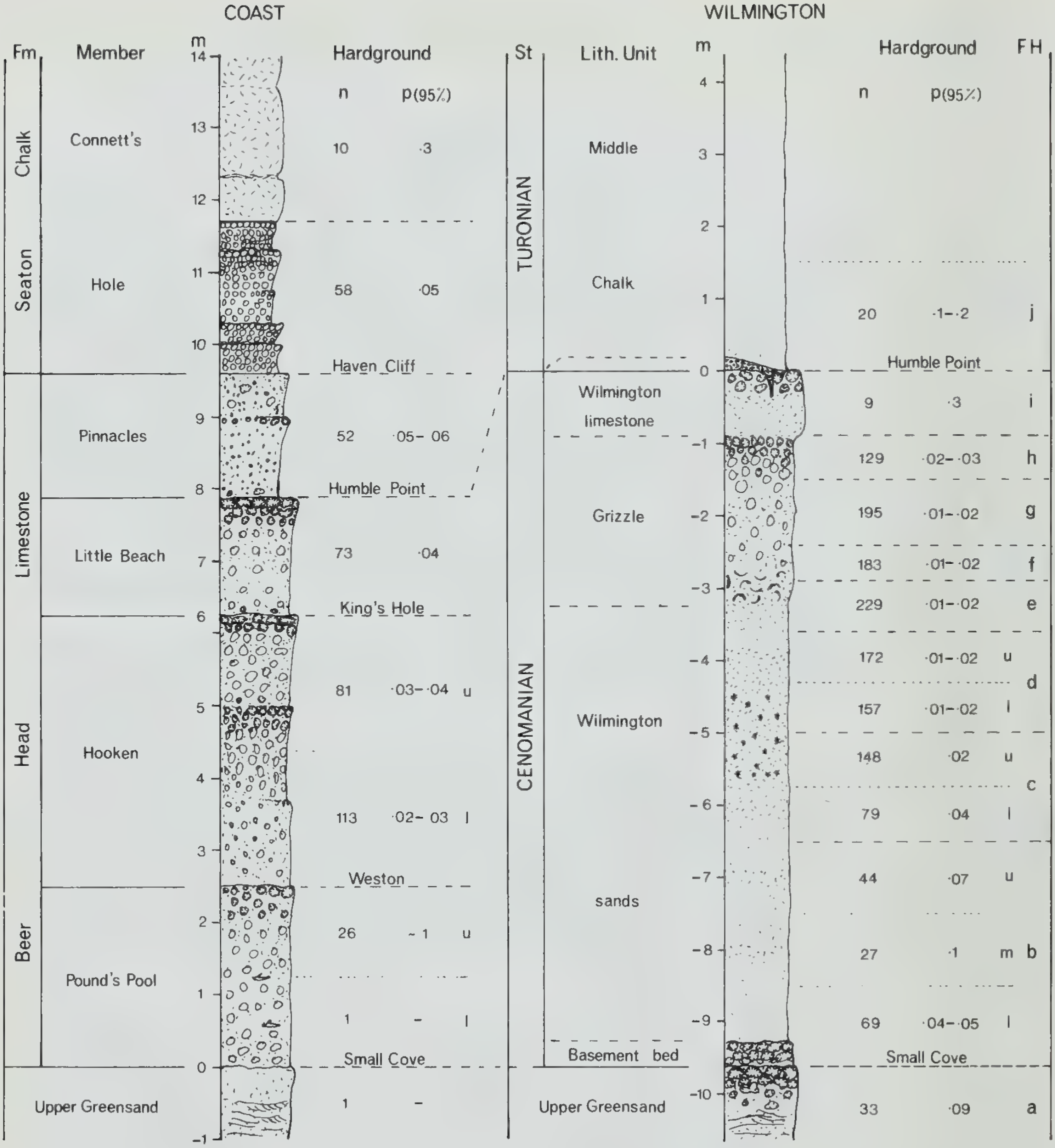

COAST
WILMINGTON
Fm
Member
m
Hardground
n
p(95%)
St
Lith. Unit
FH
Chalk
Seaton
Limestone
Head
Beer
Upper Greensand
Connett's
Hole
Pinnacles
Little Beach
Hooken
Pound's Pool
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
-1
10 ·3
58 ·05
Haven Cliff
52 ·05- ·06
Humble Point
73 ·04
King's Hole
81 ·03- ·04 u
113 ·02- ·03 l
Weston
26 ~1 u
1 - l
Small Cove
1 -
TURONIAN
CENOMANIAN
Middle
Chalk
Wilmington limestone
Grizzle
Wilmington
sands
Basement bed
Upper Greensand
4
3
2
1
0
-1
-2
-3
-4
-5
-6
-7
-8
-9
-10
20 ·1-·2 j
Humble Point
9 ·3 i
129 ·02-·03 h
195 ·01-·02 g
183 ·01-·02 f
229 ·01-·02 e
172 ·01-·02 u
d
157 ·01-·02 l
148 ·02 u
c
79 ·04 l
44 ·07 u
27 ·1 m b
69 ·04-·05 l
Small Cove
33 ·09 a

Fig. 5 Summary sections of the Cenomanian successions at Wilmington and on the coast between Beer and Branscombe, Devon, with suggested correlation. Formal stratigraphy on the coast follows Jarvis & Woodroof (1984); only informal stratigraphical terminology is used at Wilmington. n = numbers of identified echinoids recorded from each horizon. p(95%) = proportion of the fauna that we cannot be 95% certain we have not overlooked (see below for further explanation). FH = faunal horizons at Wilmington. Fm = formation. Lith. Unit = informal lithological units. m = metres. St = stages.

Suppose that *Holaster bischoffi* really existed in horizon c below our lowest record for the species (at −4·85 m), but was very rare. What are the chances that we have overlooked it? Provided the fossils are randomly preserved and distributed, the answer depends on the proportion of the fossil population that *H. bischoffi* forms at that level (i.e. its rarity) and on the total number of identifiable fossils that we have found in that horizon. If p is the probability that a specimen we find is *H. bischoffi*, and q the probability that it is not, then

$$p + q = 1 \text{ (or 100\%)}$$

because every specimen we identify is either *H. bischoffi* or it is something else. If *H. bischoffi* formed 1% of the fossil population in horizon c, p would be 0·01 and q 0·99. Every time we identify a fossil from horizon c we increase the chances of finding a specimen of *H. bischoffi*, assuming that it is really there. The total probability of overlooking the species, Q, is given by

$$Q = q^n$$

where n is the number of identified fossils recorded for horizon c. Since q is always a fraction, no matter how large, q^n declines as n increases. It is only a matter of deciding on values of q and Q to calculate the sample size (i.e. the number of fossils we need to collect and identify from horizon c) required to be reasonably sure we have not overlooked *H. bischoffi*. Shaw (1964: 109) and Paul (1982: 86) have published tables, while Hay (1972: 259) presented an extremely wide-ranging graph, of values for q and Q. Note that we can never be sure we have not overlooked a species. There is always a finite, calculable probability that we have, but for all practical purposes when this probability falls below a certain value we may ignore it. We have chosen the 95% level of confidence. Fig. 5 shows that for most of the Cenomanian section at Wilmington p lies below 0·05, often well below. Hence the ranges of most echinoids can be regarded as reasonably reliable. Note, however, that we have very small collections from the extreme base and top of the section, largely through limited exposure or inaccessibility. Paradoxically, this means that we can be highly confident that some of the rare species known only from the base or top of the section do not extend up or down into the central part, but we cannot be as sure that some abundant species which range throughout the middle of the section, *Discoides subuculus* for example, did not extend up into the Chalk or further down into the Upper Greensand.

Having discussed the adequacy of known ranges at Wilmington, we can do the same for other sections and then correlate between them. Currently the only other sections for which we know the stratigraphical distribution of echinoids with similar accuracy are some along the coast of Devon between Beer and Branscombe. The lithostratigraphy of these sections has been thoroughly redescribed recently (Jarvis & Woodroof 1984) and we have been investigating the biostratigraphy for the last three years. Fig. 5 shows a summary section with the old and new lithostratigraphic terminology. Numbers of identified echinoids and values of p at the 95% confidence level are also shown.

Shaw (1964) presented in great detail a method of correlating graphically between two sections and we have used this method. With only two principal sections, we have insufficient data to use Hay's (1972) probabilistic stratigraphical method. In graphical correlation all reliable first and last known occurrences of species are plotted as a scatter diagram with the two sections represented by the two axes of the graph (Fig. 6). A regression line is fitted to the scatter. The slope of the regression line gives the relative rate of sediment accumulation in the two sections. If both sections have identical rates, the slope of the regression line will be 45°. If a change took place in the rate of sedimentation in either or both sections, the slope of the regression line will change, as is clearly the case for the correlation between Wilmington and the coast. At Wilmington the Wilmington Sands accumulated relatively rapidly, then the Grizzle and Wilmington Limestone accumulated more slowly.

Selection of reliable points for the correlation depends on the adequacy of sampling and the rarity of specimens. Only species found in both sections can be used, but a species known from a single stratigraphically localized specimen (which represents both the first and last known occurrence) in one section is clearly unlikely to provide two accurate points for correlation. Selection of reliable points is largely a matter of common sense. We have rejected all first known occurrences of species present at the base of the section at Wilmington, because they are inherently likely, and in some cases known, to range further down. Similarly, the last known occurrences of all species from the chalk at Wilmington have been rejected since they are

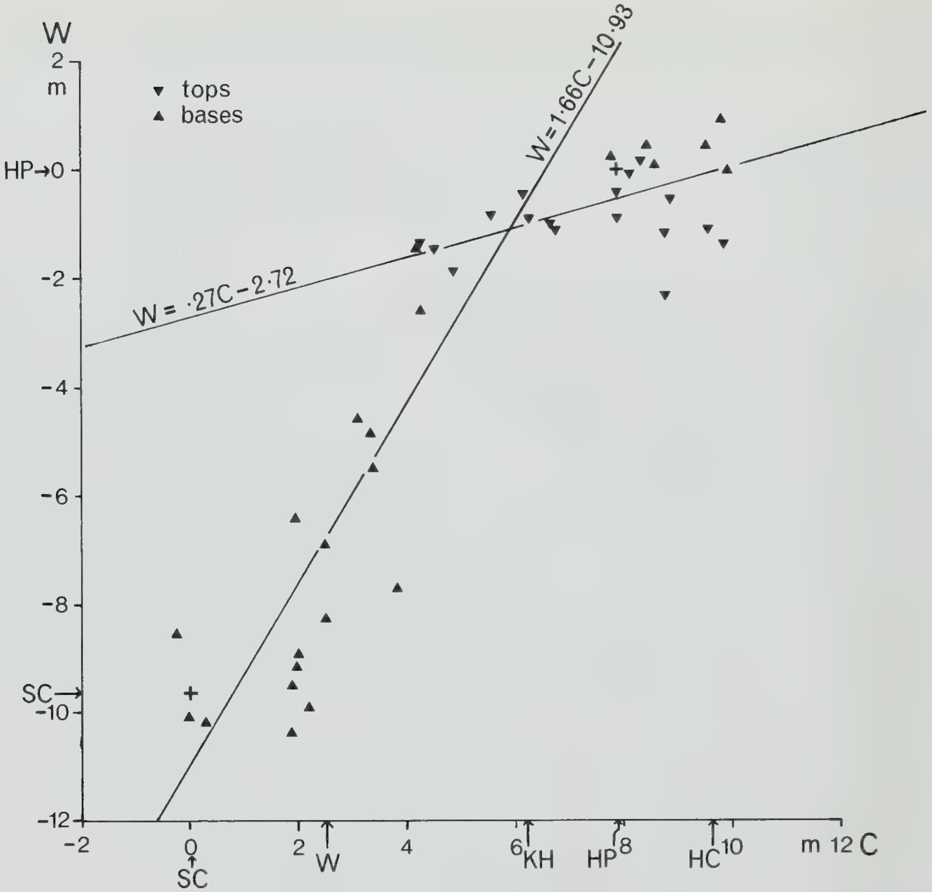


Fig. 6 Graphic correlation between Wilmington (W) and the coastal sections between Beer and Branscombe, Devon (C), based on the first and last known occurrence of echinoids. Crosses indicate positions of the Small Cove (SC) and Humble Point (HP) hardgrounds. Position of the Haven Cliff (HC), King's Hole (KH) and Weston (W) hardgrounds indicated on the coastal section. Alternative regression lines are $C = 0{\cdot}48W + 5{\cdot}93$ and $C = 1{\cdot}325W + 8{\cdot}39$. See below for further explanation.

known to range higher into the chalk on the coast where much more extensive sections occur. Finally, we have rejected all rare species, such as *Micraster distinctus*, which are known from a single stratigraphically localized specimen in one or both sections. This left us with the 40 points shown in Fig. 6, which is based on the ranges of echinoids alone.

The scatter shows two linear trends which poses the problem of fitting two regression lines. There is no *a priori* evidence as to precisely where the change in slope occurs. We have used the small central scatter in both regressions, partly to enhance the accuracy of each line by including as many points as possible and partly because there is no unambiguous way to decide which point lies on which line. A second practical problem arises from the fact that standard statistical practice regards one set of data as independent, against which the other, dependent set is correlated. In geology there is no *a priori* reason for regarding one section as providing the independent data set. In general, a more thoroughly sampled section will provide a better standard against which other, less well sampled sections can be correlated. On the other hand, the thickest succession will provide the widest scatter of points, thus controlling the slope of the regression line more closely than does a condensed sequence. To overcome this we have calculated all four possible regression lines, for both upper and lower scatters, first regarding Wilmington, then the coastal section, as the independent data set. Visually, there is little difference between the two regression lines for the lower slope, but for the upper slope regarding Wilmington as the independent data set gives a much better fit. Hence we have plotted the two lines using Wilmington as the standard section, but the equations for all four lines are given.

Fig. 6 also includes two crosses representing the two fixed points in the successions, the Small Cove and Humble Point hardgrounds. It can be seen that a straight line drawn between them is not far off the correlation suggested by the echinoids, but it does not reflect the subtle changes in sedimentaion rates at Wilmington. In the absence of unambiguous evidence for the Weston and King's Hole hardgrounds at Wilmington, the regression lines may be used to predict the levels at which they might occur.

Faunal succession

As stated earlier, with only two sections so far sampled in adequate detail we cannot apply probabilistic techniques to determine which events in the succession are reliable indications of age, and which are less reliable. Nevertheless, the fauna does seem to fall into several groupings and these are provisionally discussed here. It remains to be seen whether they will prove to be of only local significance or whether some of them can be used in wide-ranging correlation. The groupings are as follows.

(1) The oldest echinoid fauna occurs in undoubted Upper Greensand on the coast and consists of common fragments of *Pygurus* sp. and the only example of *Goniopygus* recorded from Britain. Although meagre, no trace of this fauna has been seen at Wilmington.

(2) At Wilmington the basal fauna includes *Echinogalerus faba*, *Ochetes placentula*, *Labrotaxis cenomanensis*, *Holaster laevis* and *H. revestensis*. Long-ranging species such as *Stereocidaris essenensis*, *Polydiadema bonei*, *Discoides subuculus*, *Echinogalerus rostratus* and *Catopygus columbarius* also appear at this level along with the crinoid *?Isocrinus cenomanensis*. This is probably a low Cenomanian fauna and much of it seems to come from burrow fills within the Upper Greensand. The first five species are unknown above the Small Cove hardground, however.

(3) The basal Wilmington Sands fauna includes the long-ranging forms listed above, but is distinguished by the appearance of several other common forms which are, in order of appearance: *Holaster nodulosus*, *Tetragramma variolare*, *Hyposalenia umbrella*, *Cottaldia benettiae*, *Tiaromma michelini*, and *Hemiaster bufo*, which all enter the succession in the basal 1 m or so of the Wilmington Sands. Columnals of *?I. undulatus* also first appear at this level.

(4) The upper Wilmington Sands and basal Grizzle fauna adds *Glyptocyphus difficilis*, *Labrotaxis tricarinata*, *Tylocidaris velifera*, *Allomma rhodani*, *Goniophorus lunulatus*, *Glyphocyphus radiatus* and *Cottaldia granulosa*. *A. rhodani* and *L. tricarinata* appear to be confined to this level, while *H. bufo* disappears at the top, about 50 cm into the Grizzle. *Catopygus columbarius* reaches its peak abundance at the top of this level along with the only stratigraphically localized specimen of *Micraster distinctus*. *?I. cenomanensis* is last seen in the middle of the Wilmington Sands. *Hyposalenia umbrella* and *Cottaldia benettiae* are absent from this fauna, but reappear again higher up. The next faunal change takes place just above the base of the Grizzle.

(5) The upper Grizzle fauna sees the appearance of *Hyposalenia clathrata*, common *Holaster bischoffi*, both forms of *Conulus castanea* and *Discoides favrina*. *Hyposalenia umbrella* and *Cottaldia benettiae* both reappear at the same level in the upper part of this fauna, displacing their congeners. Most long-ranging forms terminate at the top of this interval. Only *Tetragramma variolare*, *Echinogalerus rostratus*, *Catopygus columbarius* and *Holaster nodulosus* survive into the Wilmington Limestone, whence we believe our only example of *H. subglobosus* also came. The last specimens of *?I. undulatus* also occur in the Wilmington Limestone.

(6) There is then an almost complete faunal change. The two forms of *Conulus castanea* occur resting on the Humble Point hardground as limonitized and encrusted examples which

we believe are derived. Otherwise no echinoderm known from below the hardground occurs above it. The basal Turonian fauna includes *Prionocidaris granulostriata, Discoides inferus, Conulus subrotundus, Cardiotaxis cretacea, Cardiaster truncatus* and *Hemiaster nasutulus.* On the coast spines of *P. granulostriata* first appear 0·35 m above the Haven Cliff hardground, while in section 1 at Wilmington they rest on the Humble Point hardground, indicating a considerable hiatus. In the easternmost section (5) remnants of the Pinnacles Member intervene, but we have been unable to find any *Prionocidaris* spines and are unsure how thick a succession is represented here.

Other significance of stratigraphical distribution

Finally, although not strictly biostratigraphy, it is worth noting that the detailed stratigraphical distribution of some echinoids enabled us to settle their taxonomic status and evolutionary relationships more accurately. *Hyposalenia umbrella* and *H. clathrata* differ only in the nature of the pits on their apical discs. Since some echinoids are known to brood young in pits on the apical disc (see Philip & Foster 1971), our first interpretation of these two forms was as sexual dimorphs of a single species, the form with the larger pits being regarded as female. However, their mutually exclusive stratigraphical distribution, which is statistically significant at the 95% level, precludes this possibility and we have accepted them as closely similar, but distinct, species. Secondly, *H. umbrella* precedes *H. clathrata* and might be thought to be a direct ancestor, particularly since the two species are so similar in morphology. The same is true of *Cottaldia benettiae* which precedes its congener, *C. granulosa.* However, the reappearance of the earlier species of both genera at the same level in the section at Wilmington shows unequivocally that a speciation (branching) event must have occurred in both lineages and that, although not found together, the two pairs of species must have coexisted in time. Whether one was directly ancestral to the other is not known in either genus, but certainly we are not dealing with sequential species in a single lineage.

Echinoids

By A. B. Smith

Introduction

Echinoids are a conspicuous and important element in the Upper Cretaceous fauna and are abundant and diverse in the Cenomanian sands exposed at Wilmington. The basic taxonomy of British Cenomanian and Lower Turonian echinoids stems largely from work undertaken in the latter half of the 19th century. The first important contribution in this field was made by Forbes (1849–56), who described a number of the common British species and provided beautifully clear illustrations of them. This work was left uncompleted at his death and Woodward (1856) added various systematic notes to Forbes' text. The entire Cretaceous echinoid fauna was monographed by T. Wright (1864–82), and this work has remained the primary reference for British Cretaceous echinoids ever since. In the hundred years following Wright's monograph almost nothing has been written about British Cenomanian echinoids despite their diversity and abundance.

A similar situation exists on the Continent. Following the initial pioneering work by Goldfuss (1829) and L. Agassiz (1836–40), large monographic works on the Cretaceous echinoid fauna were undertaken by several palaeontologists: d'Orbigny (1854–56), Cotteau (1857–78, 1862–67), Cotteau & Triger (1857–69) in France, Schlüter (1883, 1892) in Germany and Desor (1855–58) and de Loriol (1873*a*) in Switzerland. During the present century, however, there has been little further work done on the taxonomy of Cenomanian echinoids and the most important contributions have been in some of the many short papers by Lambert (e.g. 1903, 1917) which corrected some of the taxonomic errors made by earlier workers.

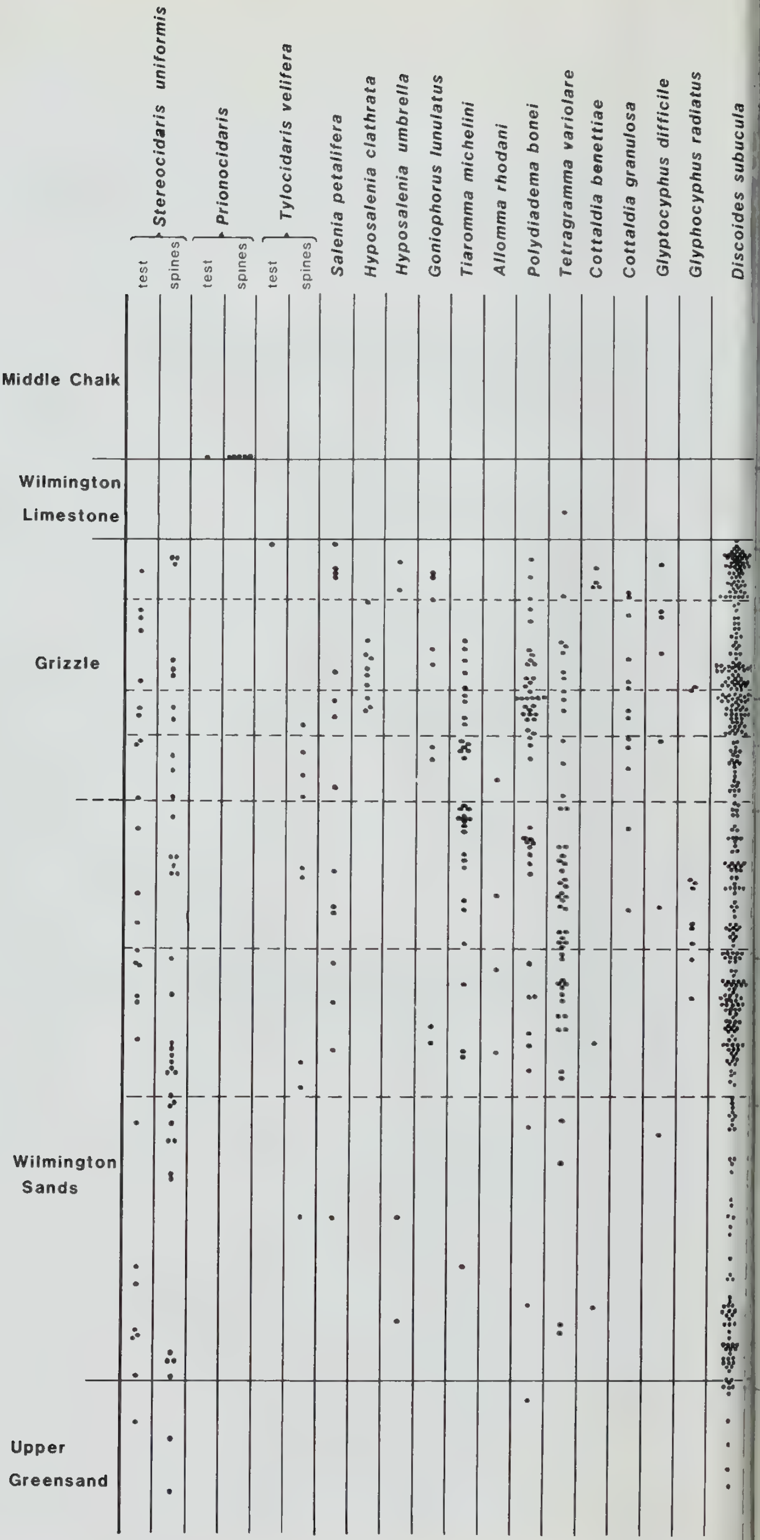
A taxonomic revision of the rich Cenomanian fauna of south-east England is therefore long overdue. This paper redescribes the species collected at Wilmington with biometrical analyses of their growth and variation, and revises their taxonomy. It illustrates the majority of species by means of stereo-pairs. It also presents an interpretation of their modes of life based on their functional morphology and gives a palaeoecological analysis of the changing species diversity.

Faunal changes and echinoid palaeoecology

The sedimentary sequence exposed at Wilmington displays a progressive change from clean, well-washed, coarse sands to very muddy sands and, finally, after a marked hiatus, to almost pure chalk. Much of this change took place during deposition of the *M. mantelli* Zone of the Lower Cenomanian. Within the succession, echinoids are not only abundant but the fauna is remarkably diverse. Thirty-six species are described here from this quarry (Table 1) and there

Table 1 Faunal list of echinoids from Wilmington, Devon described in this paper.

LOWER TURONIAN	
Cidaroida:	Holectypoida:
?Prionocidaris granulostriata	*Discoides inferus*
	Conulus subrotundus
	Holasteroida:
	Cardiaster truncatus
	Cardiotaxis cf. *cretacea*
	Spatangoida:
	Hemiaster (*Bolbaster*) *nasutulus*
UPPER CENOMANIAN	
	Holectypoida:
	Conulus castanea castanea
	Conulus castanea rhotomagensis
MIDDLE CENOMANIAN	
Stirodonta:	Holectypoida:
Tetragramma variolare subnudum	*Echinogalerus rostratus*
	Conulus castanea castanea
	Cassiduloida:
	Catopygus columbarius
	Holasteroida:
	Holaster nodulosus
	Holaster subglobosus
LOWER CENOMANIAN	
Cidaroida:	Holectypoida:
Stereocidaris essenensis	*Discoides subuculus*
Tylocidaris velifera	*Discoides favrinus*
Stirodonta:	*Echinogalerus faba*
Salenia petalifera	*Echinogalerus rostratus*
Hyposalenia clathrata	*Conulus castanea castanea*
Hyposalenia umbrella	*Conulus castanea rhotomagensis*
Goniophorus lunulatus	Cassiduloida:
Tiaromma michelini	*Catopygus columbarius*
Tetragramma variolare subnudum	*Ochetes* cf. *placentula*
Polydiadema bonei	Holasteroida:
Allomma rhodani	*Holaster laevis*
Camarodonta:	*Holaster nodulosus*
Glyptocyphus difficilis	*Holaster revestensis*
Glyptocyphus radiatus	*Holaster bischoffi*
Incertae sedis:	*Labrotaxis cenomanensis*
Cottaldia granulosa	*Labrotaxis tricarinata*
Cottaldia benettiae	Spatangoida:
	Hemiaster (*Hemiaster*) *bufo*
	Micraster distinctus


Stereocidaris uniformis
test
spines
Prionocidaris
test
spines
Tylocidaris velifera
test
spines
Salenia petalifera
Hyposalenia clathrata
Hyposalenia umbrella
Goniophorus lunulatus
Tiaromma michelini
Allomma rhodani
Polydiadema bonei
Tetragramma variolare
Cottaldia benettiae
Cottaldia granulosa
Glyptocyphus difficile
Glyphocyphus radiatus
Discoides subucula
Middle Chalk
Wilmington Limestone
Grizzle
Wilmington Sands
Upper Greensand

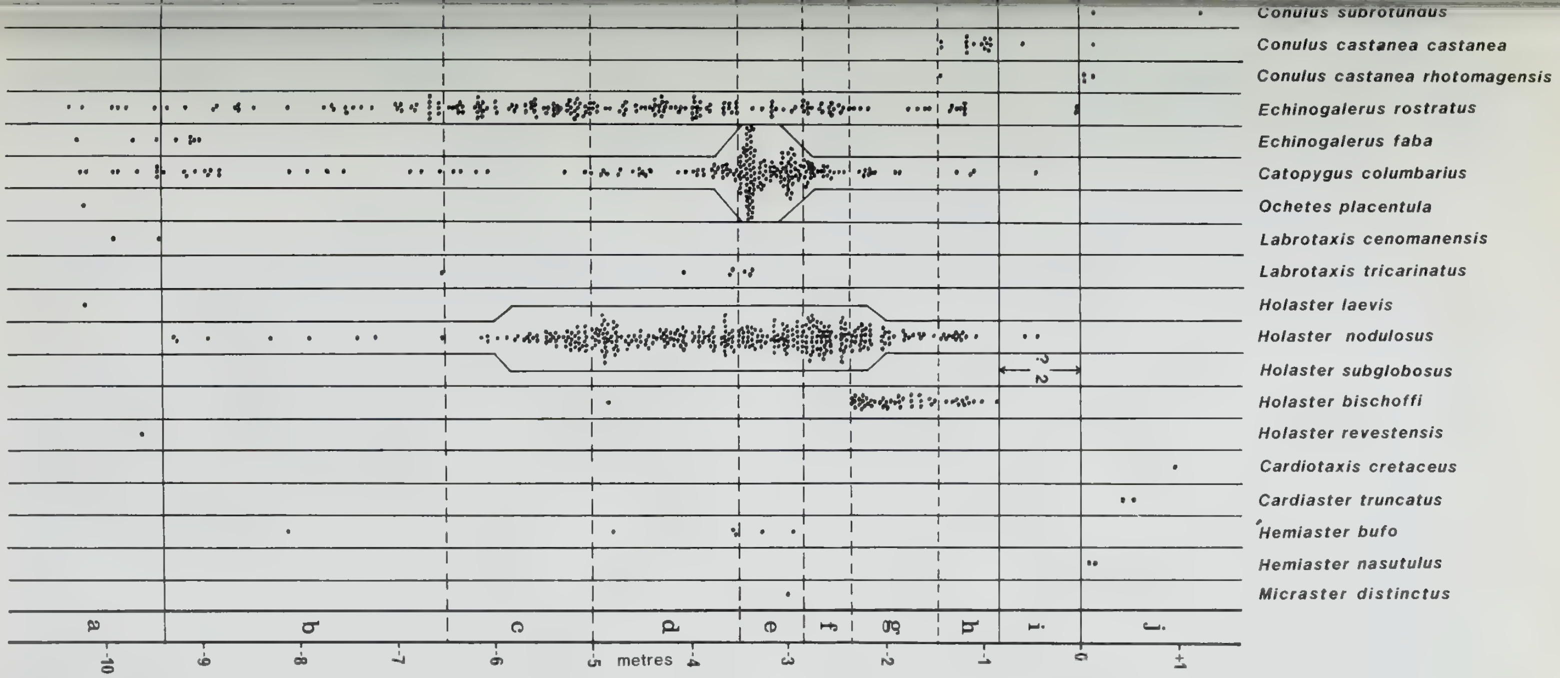


Fig. 7 Stratigraphical distribution of echinoid species at Wilmington. Each dot represents a single specimen located accurately within the succession. Divisions a to j are arbitrary divisions made solely for the purpose of analysing the faunal changes quantitatively.

are at least three other species that are known to occur but which I have not yet collected *in situ*. This is by any standard a large fauna and one of the major aims of this project was to discover the exact stratigraphical range of each species. Some 1800 individuals were collected *in situ* and their stratigraphical horizons recorded in centimetres. From this data base, broader ecological and evolutionary questions can be examined. For example, do different species dominate the fauna at different horizons and can this be correlated with the prevailing sedimentary conditions? In species which range through a significant portion of the succession it is possible to demonstrate that any evolutionary change has occurred and is the change rapid or gradual? These and other questions are examined in this section.

Obviously it is important to be sure that the echinoid fauna has not been transported far and is preserved more or less where it was living. Not a single specimen was collected that still had associated spines, while a fair proportion of individuals had some encrusting epizoans; this suggests that the dead tests lay exposed on the sea floor for some time. However, echinoid tests disaggregate readily after the soft tissue has started to decay and can withstand little transportation. The preponderance of whole tests throughout the succession therefore strongly suggests that the echinoids are preserved more or less where they had lived. The precise horizon of individual specimens is almost certainly not exactly as stated because of errors in measuring and correlating the sections, and of synsedimentary translocation of the dead test within the upper layers of the sediment by bioturbation. However, I would expect that individual specimens are accurately located to within ±10 cm of the horizon in which they lived. The only difficulty in determining the horizon of specimens is found in the Wilmington Limestone, as this is cut by fissures piping specimens well below the horizon at which they lived.

The distribution of each species (Fig. 7) has been plotted against the composite geological section (Fig. 4, p. 8). Before attempting to interpret species distribution in ecological terms it is necessary to have some idea of how individual species lived. This can be deduced from the functional morphology of the test; a brief synopsis of the autoecology of each species is given below.

Modes of life

Regular echinoids. These are almost without exception epifaunal and wander over the sea floor in search of food. In comparison with irregular echinoids, they are generally much less adapted to the type of sediment on which they live although it is possible to infer which species were adapted for shallow-water rocky bottoms (Smith 1984).

The cidarids *Stereocidaris* and *Tylocidaris* lack well-developed conjugate isopores and therefore probably had simple cylindrical tube feet (see Smith 1978). Cidarids rely on their large spines to deter predators and both *S. essenensis* and *T. velifera* probably lived quite openly on the sea floor like extant cidarids. The same is true of the saleniids *Salenia*, *Hyposalenia* and *Goniophorus* which, like the cidarids, had relatively large interambulacral spines and simple, suckerless aboral tube feet. Living cidarids and saleniids are very generalized omnivores (Lawrence 1975) capable of utilizing a wide variety of foods though not specialized for rasping. It is hard to see how any niche partitioning, save that of size, could exist between these species.

The pseudodiadematids are represented by species of *Allomma*, *Polydiadema*, *Tetragramma* and *Tiaromma*. Both *Polydiadema bonei* and *Tetragramma variolare* have a flattish oral surface and their ambulacral pores become slightly larger and more closely packed adorally, whereas in *Allomma rhodani* and *Tiaromma michelini* the peristome is deeply sunken and ambulacral pores remain widely spaced right to the peristome. The presence of phyllodes in *P. bonei* and *T. variolare* suggests that both species had oral tube feet that were capable of providing a firm grip, and that they fed by rasping with their lanterns. Neither had suckered tube feet sufficiently numerous or strong for them to have inhabited turbulent shallow-water rocky bottoms, and presumably they preferred stable sedimentary bottoms where they could graze on encrusting epizoans or free-standing algae. The flattened wheel-shaped profile of *P. bonei* and *T. variolare* presumably gave increased stability on sedimentary bottoms where tube feet could not provide anchorage in currents. *Tetragramma* has a large number of spines for locomotion and also has crowded ambulacral pores adapically. As the aboral area is devoid of large spines, *Tetragramma* may have used its aboral tube feet to cover itself with loose material for camouflage.

Neither *Allomma* nor *Tiaromma* had enough adoral tube feet to provide the grip necessary for the lantern to be used efficiently in rasping. The peristome is deeply sunken and adoral pores are small, widely spaced, and with little muscle attachment area. Indeed ambulacral pores are slightly closer together at the ambitus than they are around the mouth. These species were not adapted to gather food by rasping, but presumably fed on suitable sediment or other bottom material collected by the oral tube feet and lantern. *Allomma* had, to judge from the size of its tubercles, very large ambital spines for defence, and numerous small oral spines presumably for greater efficiency in moving over unconsolidated sediments. *Tiaromma michelini* is less specialized and has rather small, uniformly-sized tubercles (and spines). Ambulacral pores are similar on both sides and aboral tube feet were probably suckered. *T. michelini* could possible have covered itself for camouflage.

The camarodonts *Glyptocyphus* and *Glyphocyphus* are both small and unspecialized. Both have phyllodes, though poorly developed, and presumably fed by grazing with their lantern. Both also had a canopy of relatively short and uniformly-sized spines, and adapical ambulacral isopores indicate that aboral tube feet were probably suckered. These small echinoids probably lived well camouflaged.

Finally, *Cottaldia* has weak phyllodes and presumably fed in the same way as the camarodonts by grazing with the lantern. *Cottaldia* is rather unusual in possessing very dense and uniformly-sized tuberculation and its aboral canopy of spines must have been dense. Such a canopy is typically developed as an adaptation for living infaunally, where the spines can maintain a surrounding envelope of water by preventing sediment from falling between the spines (see Smith 1984). Possibly *Cottaldia* lived part of the day hidden beneath the sediment, emerging only to feed. It was certainly very poorly adapted either for burrowing through the sediment or for coping with a diet of sediment.

Holectypoids. Discoides is the most abundant echinoid found at Wilmington and is represented by three species, *D. subuculus*, *D. inferus* and *D. favrinus*. In profile all three have a broad base, low ambitus and a domed apical surface which probably enhanced their stability on unconsolidated sediment. The peristome is moderately large and has buccal notches showing that *Discoides* had well-developed compensation sacs. Internally there is a perignathic girdle. All suggest that *Discoides* had an active protrusible lantern. The periproct is large and oral in position, suggesting that *Discoides* had to cope with a considerable volume of faecal discharge, probably as a result of a sediment-rich diet. Ambulacral pores are identical over the whole test and their structure indicates that the associated tube feet were cylindrical and terminated in a suckered disc. There were no concentrations of tube feet adjacent to the peristome, so *Discoides* is unlikely to have collected its food using tube feet and probably did so with its lantern. No respiratory tube feet were developed. Oral tubercles in *D. subuculus* have a weak areole enlargement showing that the oral spines had a radially-directed power stroke. These spines were presumably used for excavating sediment from beneath the individual. Apical tuberculation is sufficiently dense and uniform in *D. subuculus* to have allowed this species to burrow in sands. Morphologically, *D. subuculus* is very like *Holectypus depressus*, whose functional morphology has been analysed by Smith (1984), and probably had a very similar life style. It was certainly not adapted for burrowing laterally through the sediment and probably just burrowed vertically down into it for protection from predators. It was almost certainly a deposit feeder emerging periodically to forage over the sea floor, like the living holectypoid *Echinoneus* (Rose 1978), picking up sediment and plant debris with its lantern, possibly with some assistance from the tube feet.

Echinogalerus is a small, depressed holectypoid with strong bilateral symmetry. Two species are present at Wilmington, *E. faba* and *E. rostratus*, which are morphologically very similar in all but size. In both species the peristome is very small, somewhat irregular in outline and without buccal slits. Internally there are small muscle attachment points forming a low perignathic girdle. *Echinogalerus* therefore must have had a functioning lantern, but one which was wholly internal and which functioned in exactly the same way as clypeasteroid lanterns. There is a slight differentiation in the structure of ambulacral pores in *E. faba*. Adapically, ambulacral pores are larger, with a larger lumen and no obvious attachment rim. Associated tube feet were probably thin-walled and cylindrical, whose main function was gaseous exchange. At the ambitus and adorally the ambulacral pores are smaller with a circular attachment rim and presumably bore small suckered tube feet. There is no concentration of tube feet adjacent to the peristome and a number of tube feet must have extended across the mouth because of the way in which the peristome lies sunken. In *E. rostratus* there is no apparent differentiation of adapical ambulacral pores and all tube feet may have been suckered. The periproct lies subambitally at the posterior of the test in both species. Both primary and miliary tubercles are dense and uniform in size and *Echinogalerus* must have possessed a dense, uniformly-sized spine canopy. It was therefore well adapted for burrowing in sands. On the oral surface tubercles have a weak areole enlargement to the posterior indicating that the power stroke of oral spines was directed posteriorly and that *Echinogalerus* had unidirectional locomotion. *Echinogalerus* was well adapted for living infaunally within medium- to coarse-grained sediments and, unlike *Discoides*, probably moved continuously through the sediment in search of food. It lacks the specializations necessary for living within sediments with large amounts of silt- or mud-sized particles. It was almost certainly an epipsammic grazer feeding in a very similar way to the extant clypeasteroid *Echinocyamus* (see Ghiold 1982) although, with far fewer tube feet, *Echinogalerus* could not have been so efficient. In epipsammic grazing, large sedimentary particles are held to the mouth by the tube feet and peristomial spines while the internal lantern scrapes off the surface organic coating. The difference in size between *E. faba* and *E. rostratus* suggests that the two species may have been adapted for feeding on different-sized particles. If this is so, then *E. rostratus* would have fed on smaller particles than *E. faba*.

Conulus is basically similar to *Echinogalerus* with a small, central peristome, no buccal notches and a weakly developed perignathic muscle-attachment zone for lantern muscles. Like *Echinogalerus* and as in living clypeasteroids, the lantern must have been wholly internal and relatively small. All ambulacral pores are much the same although they tend to become arranged in arcs of three adorally. Ambulacral pores have a structure that indicates that the associated tube feet were cylindrical with a terminal suckered disc. There were no adapical tube feet specialized for gaseous exchange and tube feet did not become crowded adjacent to the peristome. The peristome itself is slightly sunken and smaller tubercles adjacent to the peristome must have borne spines that formed a grille across the mouth. *Conulus* was probably another epipsammic grazer using the adoral tube feet and spines to manipulate suitable particles up to the mouth where they could be ingested or cleaned of any organic coating by the lantern. *Conulus castanea* is moderately depressed in profile and bilaterally symmetrical in outline. Aboral tubercles are moderately dense and uniform in size with an equally dense development of miliary tubercles in between. The spine canopy would have been sufficiently dense and uniform to have enabled *C. castanea* to burrow into sands or gravels. Oral tubercles are more or less symmetrical or show a weak areole enlargement towards the posterior suggesting that this species was not really adapted for burrowing continuously through the sediment but may, like the living holectypoid *Echinoneus*, have emerged periodically to forage. *C. castanea* presumably remained fairly static when buried.

C. subrotundus has a much taller and more rounded profile with a flat base. Adapical tubercles are fairly scattered and miliary tubercles are not nearly so common as in *C. castanea*. *C. subrotundus* is unlikely to have been able to burrow in medium- or fine-grained sediments and may have reverted to an epifaunal mode of life. *C. castanea rhotomagensis* is intermediate between true *C. castanea* and *C. subrotundus* and possibly represents an epifaunal variety of *C. castanea*.

Cassiduloids. There are two cassiduloids at Wilmington, *Catopygus* and *Ochetes*, of which only the former is common. Judged from the ambulacral pore structure, tube feet were highly differentiated. Adapically, both genera have well-developed petals and would have had thin-walled tube feet specialized for gaseous exchange. Adorally, ambulacral pores are crowded into phyllodes and tube feet would have been small and suckered. The peristome is small and lacks buccal slits. Internally there is no sign of a perignathic girdle. The primordial interambulacral plates are somewhat swollen to form bourrelets and are covered in small, densely-packed tubercles. A well-developed grille of spines would have covered the mouth. The presence of bourrelets and phyllodes show that *Catopygus* and *Ochetes*, like living cassiduloids such as *Cassidulus* and *Apatopygus*, were fairly unselective bulk sediment swallowers. Sediment particles were presumably collected by the phyllode tube feet and manoeuvred into the mouth with the aid of the bourrelet spines: large quantities of sediment are ingested by the living cassiduloid *Apatopygus* to extract the small quantities of organic material adhering to the grains. Dorsal tuberculation is moderately dense and uniform in size and both *Catopygus* and *Ochetes* would have had a well-developed spine canopy and been capable of burrowing in medium- to coarse-grained sediments. The bilateral symmetry in the arrangement of oral tubercles and the weak posterior enlargement of areoles show that both genera had unidirectional locomotion and burrowed constantly through the sediment. *Catopygus* has a more bullet-shaped test than *Ochetes* with a slightly rounded base, suggesting that it may have been adapted for burrowing through muddier or more cohesive sediments.

Holasteroids. There are nine species of holasteroid at Wilmington, falling into three morphological groups. These groups were presumably adapted for slightly different life styles. All nine species have an arrangement of tubercles which shows that they moved unidirectionally. As in all holasteroids there is no lantern and the peristome opens near the anterior border of the test. The peristome is surrounded by a small number of large and distinct isopores showing that phyllode tube feet were developed for gathering food. These tube feet were probably penicillate like those of the living holasteroid *Urechinus*.

Species of the first group are flat-based and have large primary dorsal tubercles. Two species belong to this group, *Holaster laevis* and *H. nodulosus*. The frontal ambulacrum is flush and the structure of the ambulacral pores indicates that tube feet were small and sensory in function. The other ambulacra are petaloid adapically and would have had flattened, thin-walled tube feet specialized for gaseous exchange. The anterior paired petals are quite noticeably asymmetrical, with the posterior column of pores (and therefore tube feet) much better developed than the anterior column. Water currents drawn down apically must have been diverted largely towards the posterior. Dorsal tuberculation is decidedly heterogeneous. The scattered large tubercles must have supported long dorsal primary spines and the sparse canopy of unequally-sized spines in these species suggests that they lived either epifaunally or superficially buried within moderately coarse sediments. These species resemble the living spatangoid *Spatangus* in their flat base, large primary spines and heterogeneous aboral tuberculation. *Spatangus* lives just beneath the surface in coarse sands and shell gravels but ploughs half buried in finer sediments. The two holasteroids probably had a similar life style and were deposit feeders using their phyllode tube feet to pick up underlying sediment.

Species of the second group are more rounded in shape and have a more uniform dorsal spine canopy. *Holaster bischoffi*, *H. subglobosus*, *H. revestensis* and *Labrotaxis cenomanensis* all belong to this group. Respiratory tube feet were well developed adapically and the petals are approximately symmetrical so that any water current must have flowed radially from the apex. The frontal ambulacrum is hardly sunken and tuberculation is only slightly differentiated. Ambulacral pore structure shows that the tube feet in ambulacrum III were small and sensory in function. Dorsal tubercles are small, moderately dense and uniform in size and the spine canopy must have been sufficiently well developed to have allowed these species to burrow in sands. However, they have none of the adaptations necessary for living infaunally within fine-grained sediments. These species were obviously infaunal, but without tunnel-building tube feet they were probably not capable of burrowing deeply except in highly permeable sediments. They would have moved continuously through the sediment using the tube feet of the phyllodes to collect sediment particles from the floor of the burrow. The frontal ambulacrum would not have been a passageway for food.

The third group includes *Labrotaxis tricarinata*, *Cardiaster truncatus* and *Cardiotaxis creta-*

cea. These species have a modified and sunken frontal ambulacrum. *L. tricarinata* has well-developed petals and must have had flattened, thin-walled respiratory tube feet adapically. Petals are also developed in *Cardiotaxis* but are lacking in *Cardiaster truncatus*, which is a small species. Ambulacrum III is deeply sunken and has ambulacral pores which suggests that tube feet were small and sensory in function. Tubercles bordering the frontal groove must have supported spines that formed an arch across ambulacrum III. Elsewhere adapical tubercles are small, uniformly-sized and moderately dense, and the spine canopy must have been sufficient to allow these species to live infaunally within medium- to coarse-grained sediments. Although these species still had phyllode tube feet around the peristome it seems probable that most of the sediment ingested was channelled down the frontal groove from the surface. These species either ploughed through the sediment partially buried or lived just beneath the surface collecting with its phyllode tube feet the surface sediments that cascaded down the frontal groove.

Spatangoids. The two species of *Hemiaster*, *H. bufo* and *H. nasutulus*, are well adapted for burrowing. Both possess a broad peripetalous fasciole and dense uniform adapical tuberculation. *H. bufo* has well-developed petaloid ambulacra and must have had adapical tube feet specialized for gaseous exchange. Respiratory tube feet were much less well developed in the very much smaller *H. nasutulus*. Ambulacral pores of ambulacrum III within the peripetalous fasciole are large and quite different from those elsewhere on the test. They were almost certainly associated with funnel-building tube feet, to judge from their structure. Although ambulacra are depressed adapically they become flush towards the ambitus. There is therefore no channel leading to the peristome from the apical sunken zone of ambulacrum III and food must have been collected entirely from the oral surface. Ambulacral pores adjacent to the peristome are enlarged and circular in outline and *Hemiaster* undoubtedly had penicillate tube feet in its phyllodes which were used to collect sediment. There is no evidence that either species had a subanal tuft of spines and they certainly did not have special funnel-building tube feet in this region. Finally, the wedge-shaped profile of *H. bufo* and *H. nasutulus* suggests that they were excellent burrowers, well adapted for moving through more compact sediments. Because both species have an apical fasciole, tunnel-building tube feet and (by inference) a dense and effective spine canopy, they were quite clearly capable of burrowing into any type of sediment, including muds, and of constructing a mucus-lined burrow connected to the surface by a respiratory shaft. *Hemiaster* was presumably a deposit feeder, picking up suitable material from the floor of the burrow with the penicillate tube feet.

Micraster distinctus was also well developed for an infaunal mode of life. Tuberculation on the aboral surface is moderately dense with about one primary tubercle per mm^2 and there are numerous miliary tubercles packed between the primaries. Although there is no dorsal fasciole the miliary spines, if ciliate, would have been capable of creating the necessary water circulation within the burrow. Adapically petal pores are well developed, and *M. distinctus* would have had well-developed tube feet specialized for gaseous exchange. The frontal ambulacrum is slightly depressed and forms a shallow channel from the apical region to the oral surface. The adapical pores in ambulacrum III are large isopores quite different from ambital pores and these presumably bore funnel-building tube feet. There are also enlarged pores in the subanal region and *M. distinctus* must have possessed tunnel-building tube feet in this region. *M. distinctus* apparently lived infaunally and constructed both a vertical respiratory shaft and a posterior drainage tunnel. Without an adapical fasciole to produce a mucous envelope, it is hard to see how *M. distinctus* could have burrowed into fine-grained sediment unless the dense dorsal miliary spines were capable of producing a mucous layer. On the oral surface, tubercles on the plastron have a strongly enlarged areole to the posterior side of the boss, showing that plastronal spines were capable of providing a strong forward thrust. Around the peristome there are large, circular isopores that suggest there were penicillate tube feet here. *M. distinctus* was a deposit feeder using its penicillate tube feet to pick up suitable material from the floor of the burrow and transfer this into the mouth. The fact that ambulacrum III is somewhat sunken, to form a channel to the oral surface, and has a lining of dense miliary tubercles, suggests that some proportion of the material ingested travelled to the floor of the burrow down this frontal groove.

Palaeoecological analysis of species distribution

At Wilmington echinoids are not only abundant but are also ecologically diverse. The various life styles and modes of feeding used by the different species have been outlined in the preceding section and are summarized in Table 2, below. Infaunal, epifaunal and semi-infaunal species are all present, as are species that burrowed temporarily for protection. The feeding strategies employed by the different species are also diverse. There are unspecialized omnivores, grazers, epipsammic grazers, bulk-sediment swallowers and deposit feeders, some using penicillate tube feet to gather sediment from beneath and others harvesting sediment from above *via* the frontal groove (see Table 2). By having diverse feeding strategies species can avoid direct competition with one another and occupy different niches within the same habitat. However, specific feeding strategies would be better suited for some types of sedimentary bottom as compared with others, so one might expect to find those species with one type of feeding strategy dominating under particular conditions. It is the palaeoecological implications of the distribution of species in the succession at Wilmington that I shall examine here.

The stratigraphical distribution of each species is plotted in Fig. 7, pp. 18–19, in which each individual specimen is represented by a dot. This gives a visual representation of how species abundance varies stratigraphically. To quantify the changes in species abundance and diversity the succession has been subdivided into ten units, labelled a–j. The boundaries of these units are mostly taken at important faunal changes, sometimes coinciding with the appearance or disappearance of species but more often coinciding with a change in species dominance. The

Table 2 Postulated feeding strategies of echinoid species.

EPIFAUNAL		
Omnivores (without phyllodes):	grazers (with weak phyllodes):	deposit feeders:
Stereocidaris essenensis	*Tetragramma variolare subnudum*	*Conulus subrotundus*
Tylocidaris velifera	*Polydiadema bonei*	*Discoides inferus*
Salenia petalifera	*Glyphocyphus radiatus*	**Discoides subuculus*
Hyposalenia clathrata	*Glyptocyphus difficilis*	**Discoides favrinus*
Hyposalenia umbrella		
Goniophorus lunulatus		
Allomma rhodani		
Tiaromma michelini		
Cottaldia granulosa	* possibly living within the sediment but emerging to feed at the surface	
Cottaldia benettiae		
SEMI-INFAUNAL (ploughers)		
deposit feeders collecting sediment transported down the frontal groove:	deposit feeders using penicillate tube feet to collect underlying sediment:	
Labrotaxis tricarinata	*Holaster nodulus*	
Cardiaster truncatus	*Holaster laevis*	
Cardiotaxis cf. *cretacea*		
FULLY INFAUNAL (burrowers)		
epipsammic grazers:	bulk sediment swallowers:	
Echinogalerus faba	*Catopygus columbarius*	
Echinogalerus rostratus	*Ochetes* cf. *placentula*	
Conulus castanea		
deposit feeders collecting sediment using penicillate tube feet:		
Holaster bischoffi *Holaster subglobosus* *Holaster revestensis* *Labrotaxis cenomanensis*	shallow burrowers lacking respiratory shaft	
Hemiaster (*Hemiaster*) *bufo* *Hemiaster* (*Bolbaster*) *nasutulus* *Micraster distinctus*	deeper burrowers with respiratory shaft to surface	

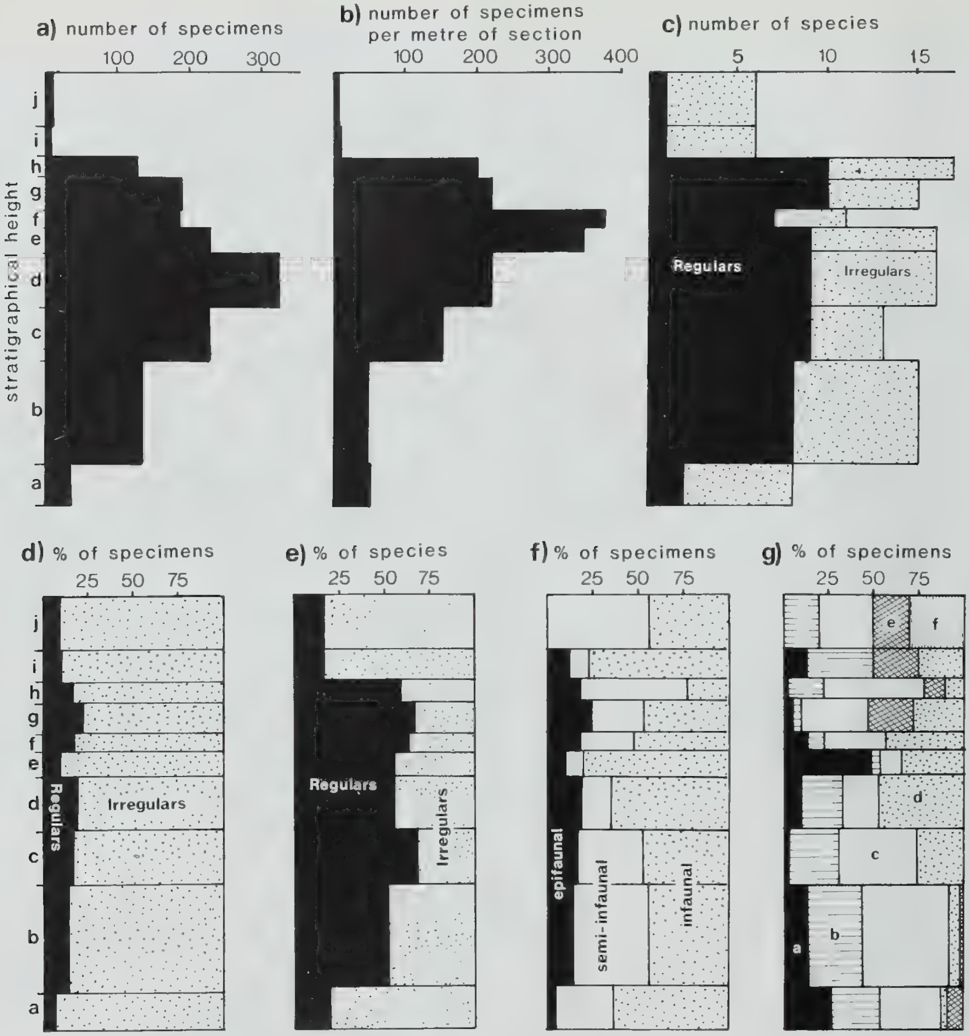


Fig. 8 Quantitative analysis of echinoid distribution within the succession at Wilmington. Units a to j are as in Fig. 5 and are drawn proportionally. **a**, number of specimens collected per unit. **b**, number of specimens collected per metre of section. **c**, number of species per unit. **d**, number of regular and irregular echinoids as a percentage of specimens collected per unit. **e**, number of regular and irregular echinoid species as a percentage of the number of species per unit. **f**, number of epifaunal, semi-infaunal and infaunal echinoids as a percentage of specimens per unit. **g**, number of specimens using specific feeding strategies as a percentage of specimens per unit (a, infaunal bulk sediment swallowers; b, epipsammic grazers; c, epifaunal and semi-infaunal grazers and omnivores; d, epifaunal and semi-infaunal deposit feeders using phyllode tube feet; e, infaunal deposit feeders using phyllode tube feet; f, infaunal deposit feeders using frontal groove to channel sediment down from above).

species composition in each unit is quantified in the final section (p. 183) and summarized in Figs 8 and 9. From this a number of general observations can be made.

(1) Regular echinoids and primarily epifaunal irregular echinoids (*Discoides*) are more uniformly distributed throughout the section than infaunal irregular echinoids. This presumably is because, generally speaking, the nature of the substratum is more crucial to species that live

within it than to species that live on it. There are several long-ranging species which are present in low numbers throughout much of the section but which become abundant only at specific horizons. This is most noticeable in *Catopygus*, but is also true of certain regular echinoids.

(2) Species diversity is moderately high throughout the Wilmington Sands and Grizzle, varying between 11 and 16 species in any one unit (Fig. 8c). Species diversity is lower in the Basement Bed and in the Wilmington Limestone and Middle Chalk where only six species are known. The lower species diversity in these units is almost entirely because of a loss of species of regular echinoids, the number of species of irregular echinoids remaining broadly similar in all units. However, the apparent paucity of regular echinoid species in units a, i and j almost certainly arises from small sample sizes. Regular echinoids are present in relatively low numbers and large sample sizes are therefore necessary to ensure that the fauna of regular echinoids is adequately sampled.

(3) Throughout most of the section there are more species of regular echinoids than species of irregular echinoids. In the Wilmington Sands and Grizzle (units b–i) 33–47% of echinoid species are irregular. This is close to the ratio of irregular to regular echinoids found living today, which Kier (1977) calculated to be 47 : 53, and suggests that a fairly representative fauna has been collected. In units a, i and j some 80% of echinoid species are irregular, but this is probably a result of the low sample sizes which are inadequate to give a representative cross section of the fauna.

(4) Although regular echinoids have a higher species diversity than irregular echinoids, their biomass is much lower (Fig. 8d). The number of specimens of regular echinoid does not exceed 23% of the total and usually lies between 10 and 20% of the total. They are least numerous at the base, where only 6% of the sample are regular echinoids. Irregular echinoid species occur in greater numbers but are less diverse.

(5) There is a very marked reduction in the size of infaunal and semi-infaunal species at the onset of chalk sedimentation. This change was brought about through paedomorphosis. The species, though small, are sexually mature and do not represent stunted individuals living in an unsuitable habitat. The reduced size is possibly an adaptation to allow burrowing or feeding in the fine-grained chalk muds. In contrast, the two epifaunal species are larger than their counterparts in the Cenomanian sands.

(6) *Discoides subuculus* is the most common and uniformly distributed irregular echinoid at Wilmington, probably because it is the most generalized feeder. It occurs throughout the Lower Cenomanian sands and is most abundant in the nodular beds at the base of unit h in the nodular upper part of the Grizzle, where almost 50% of the total number of echinoids belong to this species. *D. subuculus* is a less important element of the fauna in units f and g and towards the top of unit e where more specialized infaunal sediment feeders come to dominate.

(7) Epipsammic grazers are found throughout the Cenomanian. *Echinogalerus faba* occurs together with *E. rostratus* at the base of the section while *Conulus castanea* becomes common in the upper part of the Grizzle and is the only species found in Bed C. However, throughout most of the Wilmington Sands and Grizzle *E. rostratus* is the only epipsammic grazer and is an important member of the fauna in the coarser sands of the lower part of the Wilmington Sands, in units d, c and at the top of unit b. Epipsammic grazers were relatively successful in the lower, coarser sediments where they make up 27–30% of the irregular echinoid fauna. They became much less common in unit e and were presumably out-competed by *Catopygus* which suddenly increases at this level. Epipsammic grazers did not become a relatively important element in the echinoid fauna until the rubbly beds at the top of the Grizzle (unit h) where *Conulus castanea* appears. At this level epipsammic grazers once more make up 30% of the number of specimens of irregular echinoids.

(8) The bulk sediment swallower *Catopygus columbarius* forms a small but significant portion of the fauna of unit a (24% of the number of specimens of irregular echinoids). Above this and throughout much of the Wilmington Sands and Grizzle *Catopygus* is present but in fairly low numbers (3–14% of the number of irregular echinoids). At the base of unit e, however, *Catopygus* suddenly becomes very common, to make up almost half the number of irregular echinoids, while other echinoids such as *Tiaromma* and *Echinogalerus* become scarce.

Catopygus rapidly declines in importance once again above this level, falling to less than 10% of the irregular echinoid fauna. Presumably at the base of unit e conditions became ideal for bulk sediment swallowers and *Catopygus* was successful for a short period. Precisely what these conditions were is hard to say but at this level the sediment is a moderately well sorted medium-grained sand with approximately 20% of the particles finer than 3·75 ∅. Bulk sediment swallowers are absent from pure chalk sediments.

(9) Burrowing spatangoids able to construct a respiratory shaft to the surface are not common in the Cenomanian sands. This is presumably because the sediment was sufficiently permeable for a respiratory shaft to be unnecessary. The few specimens are mostly found near the base of unit e and the top of unit d, at the level at which *Catopygus* becomes dominant. They are also found in the Turonian Chalk.

(10) Semi-infaunal or shallow infaunal deposit feeders with a sunken frontal groove for sediment collecting are also uncommon in the Cenomanian sands, although they appear to be an important member of the chalk fauna. In the Cenomanian sands they appear at the same level as the funnel-building spatangoids and the increase in *Catopygus*. The high diversity of species of irregular echinoids at this horizon suggests that conditions were very favourable for all sorts of sediment feeders.

(11) The only common semi-infaunal or shallow infaunal deposit feeder using phyllode tube feet to collect nutrients is *Holaster*. In the coarse basal sands burrowing species of *Holaster* and *Labrotaxis* form 9% of the total number of irregular echinoids. Above this they are almost totally absent until *Holaster bischoffi* appears in unit g and forms 24% of the number of irregular echinoids. Throughout the major part of the Wilmington Sands and the lower part of the Grizzle it is the flat-based *H. nodulosus* that dominates and forms an important element of the fauna. It becomes less important with the appearance of *H. bischoffi* although it continues through to the Middle Cenomanian limestone. *H. nodulosus* is less well adapted for burrowing and is more likely to have been a semi-infaunal plougher. *H. nodulosus* was very successful throughout a considerable part of the succession, becoming a major element in the fauna in the upper part of unit c and only starting to decline in unit g. The sudden abundance of *Catopygus* at level e did have a detrimental effect on *H. nodulosus*, but only for a short time.

(12) The distribution of regular echinoid species is generally more uniform than that of irregular echinoids and species such as *Stereocidaris essenensis* appear to be scattered throughout the section. Some faunal changes can, however, be picked out. First of all there are changes in the relative abundances of the three principal pseudodiadematids (*Tiaromma michelini*, *Tetragramma variolare* and *Polydiadema bonei*) up the succession (Fig. 9). Throughout much of the Wilmington Sands up to the lower part of unit d the flattened and spinose *Tetragramma variolare* dominates over the other pseudodiadematids. Above this, for a short period during the upper part of unit d and throughout unit e it is *Tiaromma michelini* that is relatively abundant. This coincides with the rapid increase in numbers of *Catopygus* and the general diversity of selective deposit feeders. As discussed in the preceding section, *T. michelini* is also likely to have specialized as a deposit feeder since, unlike *Tetragramma* or *Polydiadema*, it had a deeply sunken peristome and no phyllodes. In unit f and in the lower part of unit g, *Polydiadema bonei* becomes the dominant pseudodiadematid. This species has better-developed phyllodes than any other Wilmington regular echinoid and presumably fed by rasping with its lantern. Although all three species occur throughout the Lower Cenomanian, their relative abundances change quite markedly, presumably marking changes in the environment favouring one or other of the different feeding strategies.

Another type of change is shown by the species of *Hyposalenia* and *Cottaldia*. In the lower part of the Wilmington Sands the few specimens that have been found all belong to the species *Cottaldia benettiae* and *Hyposalenia umbrella*. These are replaced by *Cottaldia granulosa* (from about 500 cm below datum) and *Hyposalenia clathrata* (from 260 cm below datum), which become moderately common within the Grizzle. However, at about 130–140 cm below datum, *C. granulosa* and *H. clathrata* disappear to be replaced by *C. benettiae* and *H. umbrella* once again. Quite what this change signifies is unknown but it seems more than coincidental that the change takes place at the same level in the two species.

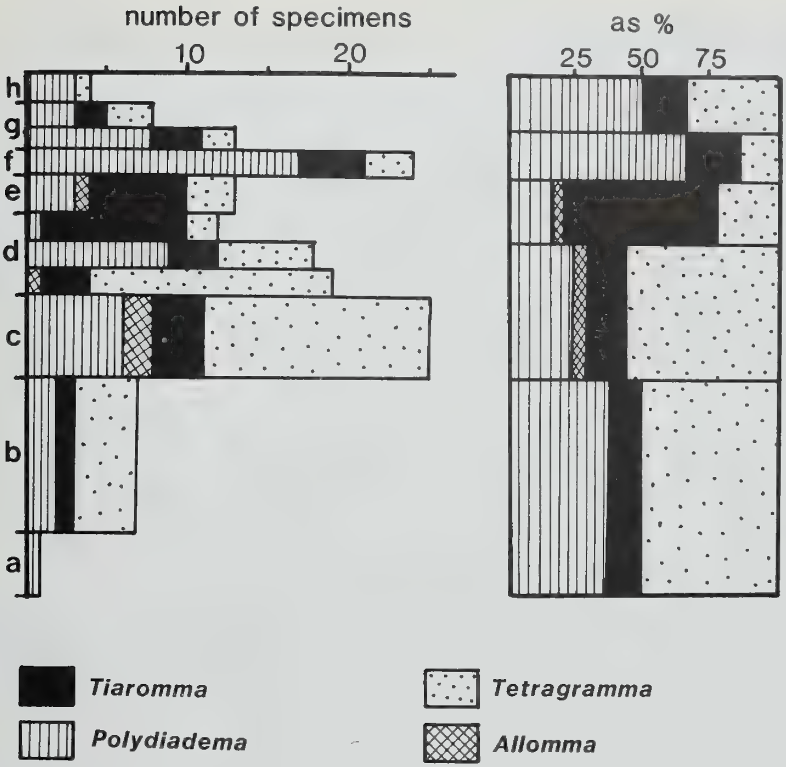


Fig. 9 Quantitative analysis of the distribution of the four species of pseudodiadematid present at Wilmington. Units a to h are as in Fig. 5 and are drawn in proportion.

The changes in the abundance and species composition of the echinoid fauna collected from this stratigraphical succession are summarized in Figs 7–9. The composition of the echinoid fauna changes markedly at two levels, one at around 900–940 cm below datum level and the other at zero datum level. The second of these coincides with a major break in sedimentation and the overlying muds were inhabited by a fauna quite different from that found in the muddy sands of the Cenomanian. Throughout the Wilmington Sands and Grizzle, however, species composition does not really change, although the relative abundance of each species is highly variable. The two species that do make an apperance towards the top of the Grizzle (*Conulus castanea* and *Holaster bischoffi*) appear suddenly in the succession without obvious antecedents and almost certainly migrated in when conditions at Wilmington became favourable. Indeed, one of the species, *Conulus castanea*, is known from the Albian of France and its sudden appearance in this section towards the top of the Grizzle can only be through migration. The variation in relative abundance of the different species within this part of the succession is therefore best seen as resulting from changing environmental conditions.

At the base of the section there is a moderately diverse fauna of sediment-feeding irregular echinoids and an unusually low proportion of epifaunal forms, particularly regular echinoids (though this may be partially the result of rather small sample size). This fauna is replaced in the lower part of the Wilmington Sands by one dominated by the generalist feeder *Discoides*, together with the epipsammic grazer *Echinogalerus*. These continue through the succession but in reduced numbers and from about half way up the Wilmington Sands it is the selective deposit feeder *Holaster nodulosus* that dominates. At the very top of the Wilmington Sands the bulk sediment swallower *Catopygus columbarius* replaces *H. nodulosus* for a short period as the most abundant species. At about this level various other types of sediment ingesters such as

Micraster, *Hemiaster bufo*, *Labrotaxis tricarinata* and *Tiaromma michelini* are also found, suggesting that at this particular period conditions must have been highly favourable for this type of feeding.

In the Grizzle we see the reverse of the faunal progression present in the Wilmington Sands. *Catopygus* rapidly decreases in importance above the base of the Grizzle while the selective deposit feeders *Holaster nodulosus* and *H. bischoffi* become the most important elements in the fauna. *H. nodulosus* apparently had a wider environmental tolerance than *Catopygus*, to judge from their relative stratigraphical ranges. Towards the upper part of the Grizzle, where coated and encrusted nodules become more and more common, first *H. nodulosus* and then *H. bischoffi* become much less important. Their places are taken by the generalist *Discoides* and the epipsammic grazer *Conulus castanea*. Finally, in the overlying Wilmington Limestone, the echinoid fauna returns once more to a moderately diverse assemblage of sediment-feeding irregular echinoids, although the small sample size makes it rather unlikely that what we have is truly representative.

Predation and parasitism

(1) *Predation*. Only two of the many hundreds of specimens collected at Wilmington show convincing evidence of having been preyed upon by gastropods. One is a specimen of *Catopygus columbarius* (E.80703) from the top of the Wilmington Sands, 345 cm below standard datum level. This has a slightly irregular oval hole, 1·8 × 1·5 mm in diameter, through the phyllode of ambulacrum III. The sides of this bore hole are more or less vertical and slightly concave in places. The other is a specimen of *Conulus castanea castanea* (E.80890) which was collected loose but presumably came from the upper part of the Grizzle. This shows a slightly larger ovoid hole, 2·2 × 1·8 mm in diameter with slightly less regular walls, which pierces interambulacrum 1 at the ambitus.

In both cases the holes are clean and sharp bore holes. The absence of any abnormal stereom growth around the perforations shows that they were lethal and were drilled by predators. Many gastropods are known to attack echinoids by drilling through the test (see Hughes & Hughes 1971, Sohl 1969). The bore holes in the two Wilmington specimens are slightly less circular than those produced by predatory gastropods today but were also probably produced by gastropods. Although borings by predatory gastropods in molluscs are known as far back as the Albian (Taylor, Cleevely & Morris 1983), these are the earliest reported attacks on echinoids. Because such a small proportion of the echinoids collected from Wilmington show evidence of gastropod predation (probably about 0·1% of the fauna), either echinoids were not a usual part of the gastropod's diet, or the species of predator was only a rare immigrant into this habitat.

The only other evidence of predation comes from a specimen of *Holaster subglobosus* (E.80284) from the Wilmington Limestone (Pl. 40, fig. 1). This has one large and two smaller depressed patches on the test which are repairs to test damage. The repaired patches are rather irregular in outline, the largest being 6 × 3 mm, with floor and vertical walls covered in tubercles. This specimen was probably attacked by a shark or some other predatory fish which managed to pierce the test but not crush it. The echinoid survived the attack and was able to repair the irregular holes produced by the predator by regenerating the test.

(2) *Parasitism*. Ten deformed and parasitized specimens have been collected at Wilmington. Surprisingly, although irregular echinoids are much more numerous than regular echinoids in this section, it is only regular echinoids that show evidence of parasitism. Two styles of parasite-induced deformation are recognizable in Wilmington specimens. The more common is where a single interambulacrum has become abnormally swollen. In extremely deformed specimens slit-like holes are present at sutures (Pl. 40, figs 2, 3), although these are not caused by an external parasite but by abnormal growth. The fact that it is always an interambulacral zone which is swollen and distorted suggests that the deformation is produced by an internal parasite within one of the interradial gonads. Several groups of invertebrates parasitize the

gonads of echinoderms (see for example Barel & Kramers, 1977) but precisely which group could produce such extreme deformation is unknown. The preferred host is *Polydiadema bonei*, since five specimens (E.81329–33) of this species have been attacked out of a total of about 260 examined. However, other species display an identical deformation. Two specimens of *Glyptocyphus difficilis* (E.80033, E.81326) are similarly deformed, both coming from about 160 cm below standard datum level. A specimen of *Hyposalenia clathrata* (E.81172) also has a deformed interambulacrum with a prominent slit-like hole interradially on the oral surface.

The second type of deformation also produces swollen and distorted zones on the test but these are associated with relatively small circular holes piercing ambulacral zones and positioned ambitally (Pl. 40, fig. 4). In both specimens showing this type of deformation, more than one ambulacrum has been pierced. There is some abnormal stereom deposition around the holes. The injuries are almost certainly produced by parasitic gastropods that remained attached to the outside of the test for the remainder of the animal's life. All Recent parasitic gastropods that pierce echinoid tests belong to the family Eulimidae (Waren, *in* Kier 1981) and this type of abnormality has been reported from an Upper Albian *Hemiaster* by Kier (1981). Only *Glyphocyphus radiatus* shows this type of parasite-induced deformation and two specimens (E.81327, E.81328) out of the forty or so examined had been attacked. In both cases therefore approximately 5% of the population were parasitized.

Evolutionary changes

Microstratigraphical collecting through the richly fossiliferous succession of Lower Cenomanian sands spanning two subzones has provided an ideal opportunity to investigate whether species could be shown to be undergoing gradual evolutionary change within the sequence. Each species was carefully examined to see if any detectable change had occurred within its range at Wilmington. Some were represented by sufficient numbers to be treated biometrically, in which case a wide range of parameters was plotted against the stratigraphical position of the specimens. This was not possible for the majority of species which are present in relatively small numbers and these could only be treated subjectively.

Within the ranges of most species there was no discernible morphological difference between the stratigraphically oldest and youngest specimens. No species of regular echinoid showed any evidence of undergoing gradual evolutionary change although several are quite long-ranging. A few species of irregular echinoid did, however, show some stratigraphical variation and it is these examples that I shall discuss here.

(1) *Discoides subuculus*. Variation in this species has been analysed and discussed elsewhere (Smith & Paul 1985). Gradual change was observed in the relative height of the test which was interpreted as ecophenotypic variation.

(2) *Echinogalerus rostratus*. This is a long-ranging species that occurs throughout the whole of the Lower Cenomanian succession and is also present in the Middle Cenomanian. It is very similar to juveniles of *E. faba*, which also occurs near the base of the succession at Wilmington, and the two species are undoubtedly closely related. Whether *E. faba* arose from *E. rostratus* through hypermorphosis or *E. rostratus* arose from *E. faba* through neoteny or both stemmed from a third species is impossible to tell since both species already coexist at the base of the section. *E. rostratus* provides good evidence of having undergone a gradual morphological change through time. Specimens from near the base of the section tend to be weakly rostrate with the periproct opening posteriorly, have a flat or lightly concave oral surface and (for *Echinogalerus*) a moderate-sized peristome. Specimens from towards the top of the species range are usually strongly rostrate so that the periproct is subambital and faces downwards, the oral surface is lightly convex and the peristome is smaller.

To quantify these changes and search for other possible changes, all moderately- to well-preserved specimens with accurate stratigraphical data were analysed biometrically. Quantifying the change in relative size of the peristome was straightforward. The ratio of peristome length to test length for each specimen was calculated and plotted against stratigraphical height

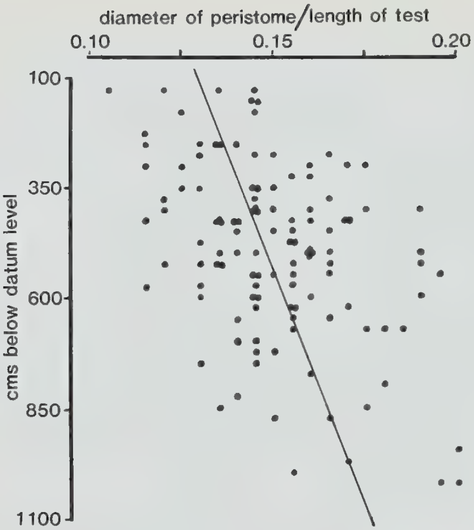


Fig. 10 Quantitative analysis of variation in peristome size for *Echinogalerus rostratus* within the succession at Wilmington. Each dot represents one specimen accurately located within the succession. Regression analysis of this data gives a correlation equation of $P = 0{\cdot}129 + H$ where P = diameter of peristome/length of test and H = distance beneath datum level in centimetres.

(Fig. 10). This gave quite a wide scatter at any one horizon but a definite trend towards a smaller peristome size through time is discernible. Regression analysis of the graph gave the equation $Lp = 0{\cdot}129 + 0{\cdot}000043\,H$ where Lp = peristome length/test length and H = stratigraphical level.

No attempt was made to quantify the curvature of the oral surface as no obvious objective criterion for judging curvature could be used. It was, however, possible to assess the extent of rostral development in individual specimens. Specimens were assigned to one of three categories by visual inspection; those with little or no rostral development in which the periproct opens posteriorly and is more or less hidden in oral view, those with a moderate rostral development in which the periproct is subambital and partially visible from the oral surface but which still faces more towards the posterior than towards the oral surface, and thirdly those with a prominent rostral development which have a subambital periproct that faces downwards rather than towards the posterior. A histogram of these categories plotted against stratigraphical position was then drawn up (Fig. 11). This shows that there is a definite though rather irregular increase in the proportion of rostrate specimens up the succession.

Echinogalerus rostratus appears to show gradual morphological change through time. The reduction in relative size of the peristome is readily explained in functional terms. As discussed previously, *E. rostratus* was almost certainly an epipsammic grazer, feeding on the organic particles adhering to individual grains of sediment. Now *E. rostratus* is a very small species, never exceeding 9 mm or so in length, and its peristome is not much larger than most of the sand grains between which it burrowed. The Lower Cenomanian sands at Wilmington are initially rather coarse and become finer upwards. It is therefore not surprising to find that the peristome is largest in size in specimens from the coarsest sediments and becomes proportionally smaller in specimens from somewhat finer sands. The change in the shape of the test, which seems primarily to be brought about through a shift in the positioning of the periproct, has less obvious functional significance. It may also be in response to changes in the sediment through which *E. rostratus* burrowed, but whether this was because of the increased muddiness of the sediment or some other factor is pure conjecture.

(3) *Catopygus columbarius*. Biometrical analysis of all stratigraphically located specimens of *C. columbarius* failed to reveal any significant change in morphology throughout the species' range. Variation in the parameters studied proved to be as great at any one level as it was

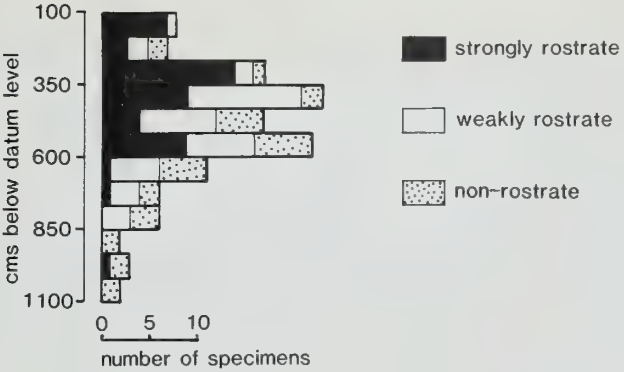
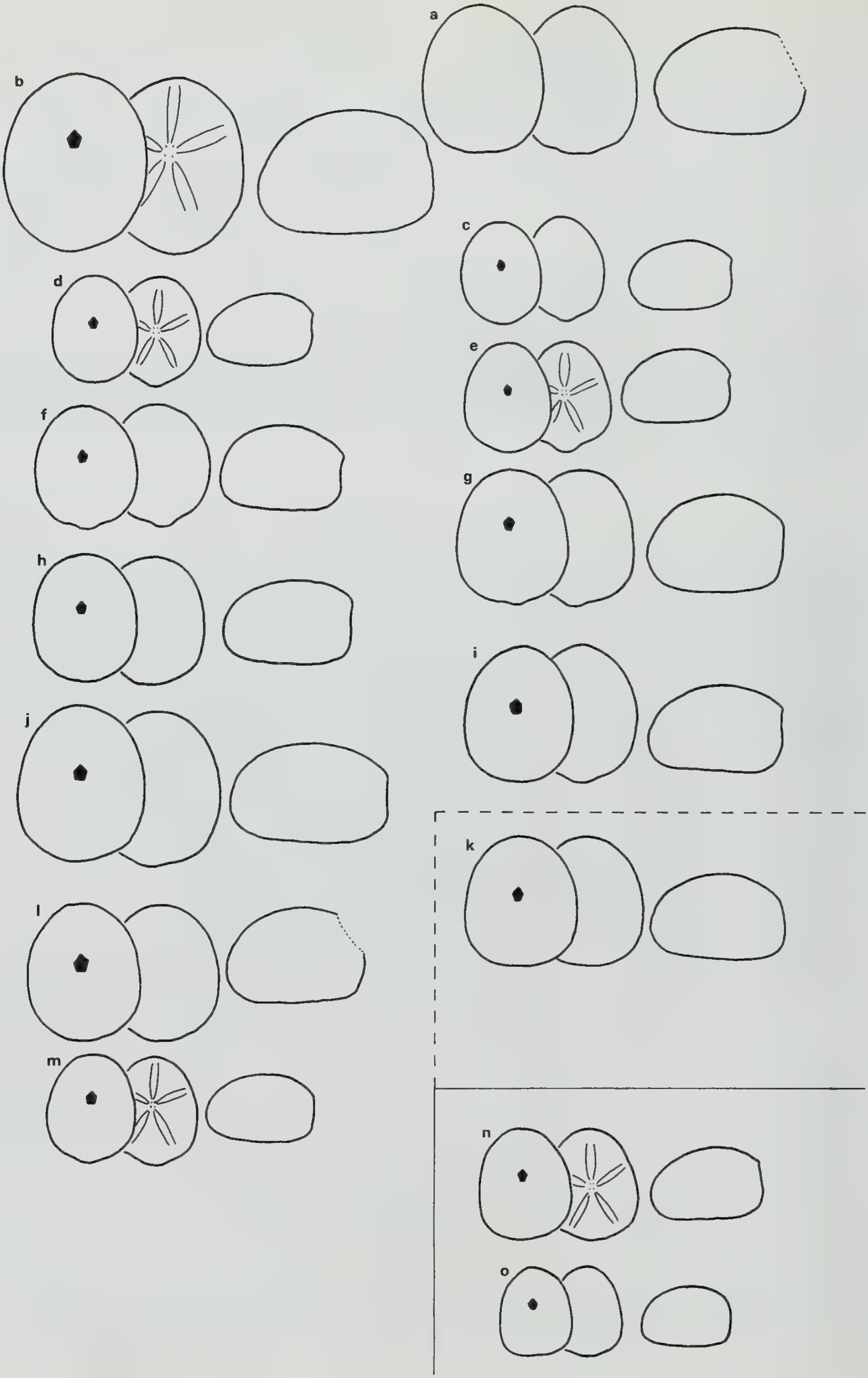


Fig. 11 Analysis of 'degree of rostrateness' in *Echinogalerus rostratus* within the succession at Wilmington. When viewed from the lower surface, specimens were classed as strongly rostrate if the periproct was clearly visible, weakly rostrate if the periproct was only just visible and non-rostrate where the periproct could not be seen.

through the succession. However, a subtle change in overall shape was noticed in the course of investigating this species. Specimens from the basal part of the succession are more squarely truncated at the posterior than those further up. Those from the basal part correspond precisely to Goldfuss' species *Catopygus carinatus*, whereas the majority, which are rather more oval in outline, correspond to Lamarck's species *Catopygus columbarius* as interpreted by Cotteau. In all other respects the two forms are identical and scarcely warrant separation. The two forms do not overlap in range. Below 940 cm below standard datum the truncated form is found whereas above this level oval forms are found. One intermediate (Fig. 12k) is found at 880 cm below standard datum but throughout the Wilmington Sands and Grizzle *C. columbarius* remains broadly constant in outline. However, in the Middle Cenomanian Limestone, the only specimen of *C. columbarius* collected once more had a rather truncated posterior to the test. These changes in profile coincide with breaks in sedimentation, while the main part of the succession between the breaks has a morphologically uniform population. The two forms may represent populations of the same species which replace one another. There is no evidence suggesting that one form is derived from the other through gradual transformation.

(4) *Holaster nodulosus.* This species appears above 940 cm below standard datum at the base of the Wilmington Sands. It replaces *H. laevis*, which occurs below this horizon and in the Upper Albian, and probably evolved from it. Apart from the lowest two specimens at the very base of the Wilmington Sands, which have an unusually flat base, a steeply inclined anterior, a sharp ambitus and are intermediate between *H. laevis* and *H. nodulosus*, specimens from throughout the Wilmington Sands and Grizzle are broadly constant. Biometrical analysis shows that, for the parameters measured, the variation at any one level is just as great as any variation stratigraphically. Towards the top of the Grizzle forms with slightly flatter bases and a more angular ambitus appear, but this subtle change proved impossible to analyse quantitatively. Complete gradation exists between tall domal forms with a well-rounded ambitus and flatter forms with an angular ambitus; these forms are interpreted here as end members of a highly variable species. The forms with flatter bases are found in the more muddy sands where *Holaster* might be expected to have had more difficulty in burrowing – they may therefore represent epifaunal forms of *H. nodulosus.*

(5) *Hyposalenia* and *Cottaldia.* Both of these genera are represented at Wilmington by two species. In both cases the species are distinct and show no intergradation. They are also stratigraphically separated; one species of each genus occurs between 140 and 500 cm below


a
b
c
d
e
f
g
h
i
j
k
l
m
n
o

standard datum (*H. clathrata* and *C. granulosa*) while the other (*H. umbrella* and *C. benettiae*) is found below and above this level but not contemporaneously. The most probable explanation for this is that these are geographically or ecologically separated pairs of species which lived contemporaneously and which replaced one another at Wilmington as conditions oscillated.

So, although most species underwent no discernible morphological change within their time range at Wilmington there are a few that did. *Discoides subuculus* and possibly *Holaster nodulosus* show a small variation in shape which may be ecophenotypic. *Echinogalerus rostratus*, on the other hand, does show a gradual change in morphology through time which is probably genetic. In addition a number of migration events can be recognized, such as the sudden appearance of *Holaster bischoffi* and *Conulus castanea*. The biostratigraphical implications of these data have been discussed in an earlier section (p. 15).

Systematic descriptions

The species of echinoids described in this paper are classified as follows.

- Subclass Cidaroidea Claus 37
  - Order Cidaroida Claus 37
    - Family Cidaridae, Subfamily Cidarinae Gray 37
      - Genus *Stereocidaris* Pomel 37
        - *Stereocidaris essenensis* (Schlüter) 37
    - Family Psychocidaridae Ikeda 40
      - Genus *Tylocidaris* Pomel 40
        - *Tylocidaris velifera* (Bronn) 40
      - Genus *Prionocidaris* Agassiz 43
        - *?Prionocidaris granulostriata* (Desor) 43
- Subclass Euechinoidea Bronn, Infraclass Acroechinoidea Smith 44
  - Cohort Echinacea Claus 44
    - Superorder Stirodonta Jackson 44
      - Order Salenioida Delage & Hérouard 44
        - Family Saleniidae Agassiz 44
          - Genus *Salenia* Gray 44
            - *Salenia petalifera* (Desmarest) 44
          - Genus *Hyposalenia* Desor 48
            - *Hyposalenia clathrata* (Woodward) 48
            - *Hyposalenia umbrella* (Woodward) 53
          - Genus *Goniophorus* Agassiz 55
            - *Goniophorus lunulatus* Agassiz 55
        - Family Pseudodiadematidae Pomel 59
          - Genus *Tiaromma* Pomel 59
            - *Tiaromma michelini* (Agassiz) 59
          - Genus *Polydiadema* Lambert 64
            - *Polydiadema bonei* Forbes 64
          - Genus *Tetragramma* Agassiz 69
            - *Tetragramma variolare subnudum* (Agassiz) 69
          - Genus *Allomma* Pomel 74
            - *Allomma rhodani* (Agassiz) 74

Fig. 12 Outline diagrams (oral, apical and lateral) of *Catopygus columbarius* from the succession at Wilmington, showing the range of variation. a–j, l, m = *C. columbarius*, *sensu stricto*; n, o = *C. carinatus* morphotype; k = intermediate form. Measurements are stratigraphical level below standard datum. a, E.80800, 43 cm; b, E.80831, 110 cm; c, E.80814, 183 cm; d, E.80800, 244 cm; e, E.80755, 348 cm; f, E.80839, 438 cm; g, E.80744, 528 cm; h, E.80834, 655 cm; i, E.80740, 753 cm; j, E.80832, 880 cm; k, E.80770, 880 cm; l, E.80747, 915 cm; m, E.80753, 938 cm; n, E.80833, 945 cm; o, E.80750, 985 cm.

Superorder Camarodonta Jackson 78
  Family Glyphocyphidae Duncan 78
    Genus *Glyphocyphus* Haime 78
      Glyphocyphus radiatus (Goldfuss) 78
 Order Temnopleuroida Mortensen 83
  Family Zeugopleuridae Lewis 83
    Genus *Glyptocyphus* Pomel 83
      Glyptocyphus difficilis (Agassiz) 83
Echinacea, family uncertain 88
    Genus *Cottaldia* Desor 88
      Cottaldia benettiae (König) 89
      Cottaldia granulosa (Goldfuss) 93
Cohort Irregularia Latreille 96
 Order Holectypoida Duncan 96
  Family Discoididae Lambert 96
    Genus *Discoides* Parkinson 96
      Discoides subuculus (Leske) 96
      Discoides inferus (Desor) 101
      Discoides favrinus (Desor) 103
  Family Conulidae Lambert 106
    Genus *Conulus* Leske 106
      Conulus castanea (Brongniart) 106
      Conulus subrotundus (Mantell) 112
  Family Galeritidae Gray 115
    Genus *Echinogalerus* König 115
      Echinogalerus faba (Desor) 115
      Echinogalerus rostratus (Desor) 120
 Order Cassiduloida Claus 125
  Family Nucleolitidae Agassiz & Desor 125
    Genus *Catopygus* Agassiz 125
      Catopygus columbarius (Lamarck) 125
  Family Cassidulidae Agassiz & Desor 132
    Genus *Ochetes* Pomel 132
      Ochetes cf. *placentula* (Desor) 132
 Order Holasteroida Durham & Melville 134
  Family Holasteridae Pictet 134
    Genus *Holaster* Agassiz 134
      Holaster nodulosus (Goldfuss) 134
      Holaster laevis (Brongniart) 142
      Holaster bischoffi Renevier 146
      Holaster subglobosus (Leske) 151
      Holaster revestensis Lambert 155
    Genus *Labrotaxis* Casey 158
      Labrotaxis cenomanensis (d'Orbigny) 158
      Labrotaxis tricarinata (Lambert) 161
    Genus *Cardiaster* Forbes 166
      Cardiaster truncatus (Goldfuss) 166
    Genus *Cardiotaxis* Lambert 167
      Cardiotaxis cf. *cretacea* (Sorignet) 167
 Order Spatangoida Claus 170
  Family Micrasteridae Lambert 170
    Genus *Micraster* Agassiz 170
      Micraster distinctus d'Orbigny 170
  Family Hemiasteridae Clark 173
    Genus *Hemiaster* Agassiz 173
     Subgenus *Hemiaster* Agassiz 173
      Hemiaster (*Hemiaster*) *bufo* (Brongniart) 173
     Subgenus *Bolbaster* Pomel 178
      Hemiaster (*Bolbaster*) *nasutulus* (Sorignet) 178

Subclass **CIDAROIDEA** Claus, 1880

Order **CIDAROIDA** Claus, 1880

Family **CIDARIDAE** Gray, 1825

Subfamily **CIDARINAE** Gray, 1825

Genus ***STEREOCIDARIS*** Pomel, 1883

Stereocidaris uniformis essenensis (Schlüter, 1892)

Pl. 1, figs 1–3; Pl. 2, figs 7–8; Fig. 13

1862	*Cidaris vesiculosa* Cotteau: 222; pl. 1050, figs 1–9, 17–20 (*non* Goldfuss).
1864	*Cidaris vesiculosa* Wright: 41; pl. 2, fig. 5; pl. 3, fig. 1 (*non* Goldfuss).
1892	*Dorocidaris essenensis* Schlüter: 133; pl. 9, fig. 8; pl. 15, fig. 8.
1894	*Typocidaris essenensis* (Schlüter) Lambert: 37; pl. 1, figs 17–18.
1909	*Typocidaris essenensis* (Schlüter); Lambert & Thiéry: 151.
1963	*Cidaris vesiculosa* Cayeux: 16, fig. 1 (*non* Goldfuss).

MATERIAL. The description and biometric study is based on eleven more or less whole coronas from the quarry at Wilmington (E.76260–2, E.76309, E.76319, E.76322–4, E.75578 and E.81267–8) together with the four whole coronas from the Lower Cenomanian greensands at Warminster (E.75742a–d) on which Wright (1864) based his description of *C. vesiculosa*. A further 22 positively identifiable coronal fragments were located accurately within the succession at Wilmington. A large number of isolated spines were also collected of which 35 were stratigraphically located within the succession.

STRATIGRAPHICAL OCCURRENCE AND DISTRIBUTION. At Wilmington, *S. uniformis essenensis* is found throughout the Grizzle and the Wilmington Sands from 114 cm below to 986 cm below standard datum level. It appears to be reasonably well distributed within this part of the succession but at no horizon is it particularly common. Elsewhere in Britain this species is found in the Lower Cenomanian greensands of the Warminster district and the Grey Chalk of Dover.

DESCRIPTION. *SHAPE AND SIZE*. The corona is circular in outline and in profile has uniformly convex sides with flattened oral and apical surfaces. Tests range in diameter from 10·6 mm to 29·8 mm (mean = 18 mm; SD = 6·2; N = 15) and in height from 5·8 mm to 20·0 mm (mean = 11 mm; SD = 4·2; N = 15). The height of the test is 55–67% of the test diameter (mean = 61%; SD = 3·3; N = 15).

APICAL SYSTEM. No plates of the apical system are preserved in any specimen examined. In diameter, the apical disc ranges from 5 mm to 12·8 mm and is 42–51% of the test diameter (mean = 46%; SD = 3·4; N = 15).

AMBULACRA. Ambulacral zones are narrow and sinuous. Their width at the ambitus is 12–14% of the test diameter (mean = 13%; SD = 0·7; N = 15) and 26–28% of the width of interambulacral zones. The ambulacral pores are narrow, partitioned isopores set slightly oblique and arranged uniserially. There is no oral/apical differentiation of the ambulacral pores. The interporal partition is raised slightly as a small knob. At the ambitus, the pore zone makes up 12–23% of the ambulacral width (mean = 18%; SD = 2·9; N = 15). The perradial zone is elevated and densely covered in tubercles arranged in distinct horizontal and vertical rows. At the ambitus the number of ambulacral tubercles in a horizontal row increases from two at 10·6 mm test diameter to eight at 29·8 mm test diameter (Fig. 13). In larger specimens the number of ambulacral tubercles decreases both adapically and adorally. All ambulacral tubercles are small and imperforate. Each ambulacral plate carries a single horizontal row of tubercles. The total number of ambulacral plates in a single ambulacral column increases from 26 at 10·6 mm test diameter to 72 at 29·8 mm test diameter (Fig. 13). Furthermore, ambulacral plates are not fixed in position relative to interambulacral plates but migrate as the test grows. The number of ambulacral plates that adjoin ambital interambulacral plate 3 increases from 11 plates at 10·6 mm test diameter to 26 at 29·8 mm test diameter (Fig. 13). Therefore, ambulacral

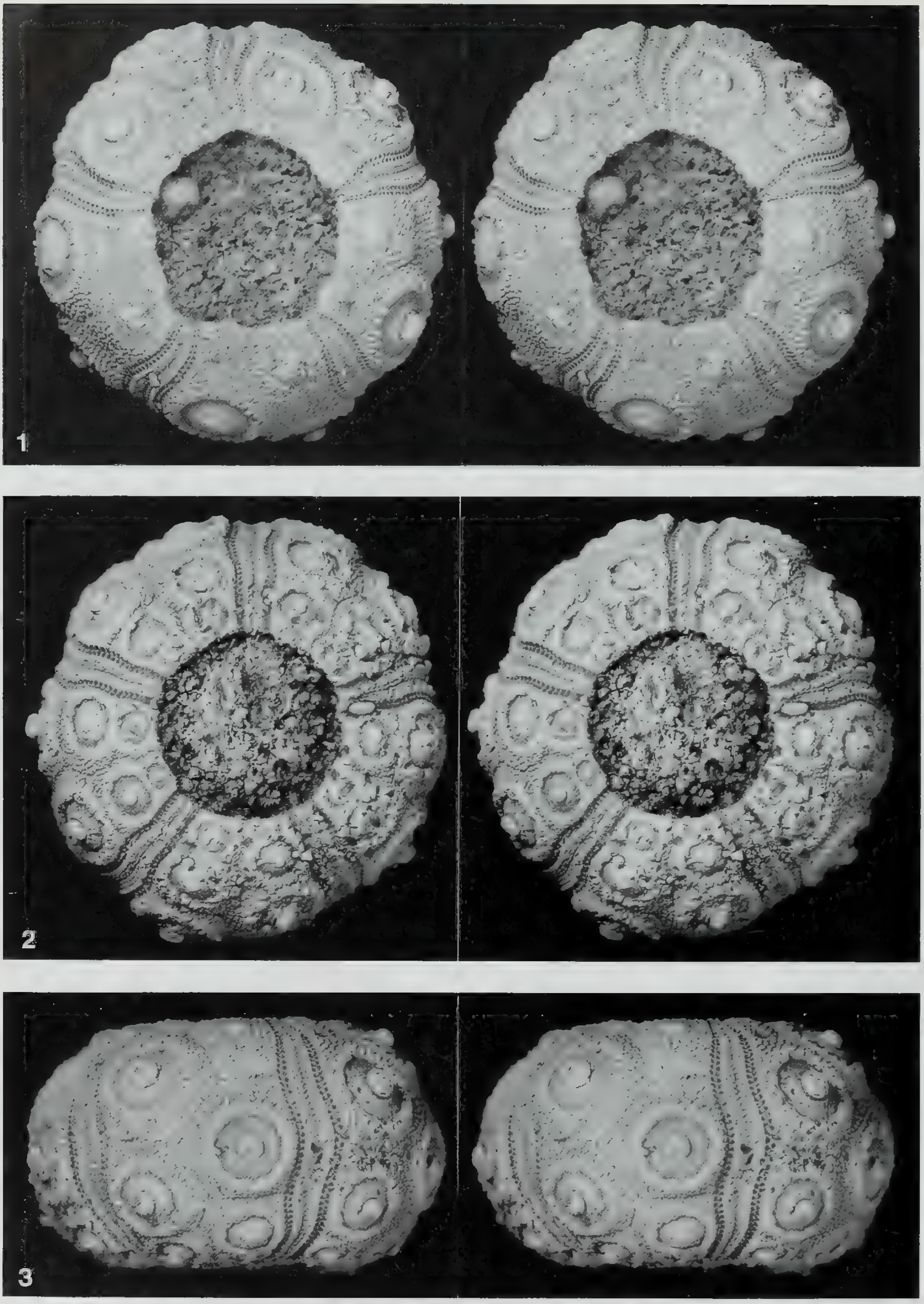


Plate 1

Stereocidaris uniformis essenensis (Schlüter)

Figs 1–3 E.76261: 1, apical; 2, oral; 3, lateral. Lower Cenomanian, White Hart sand pit, Devon (× 3).

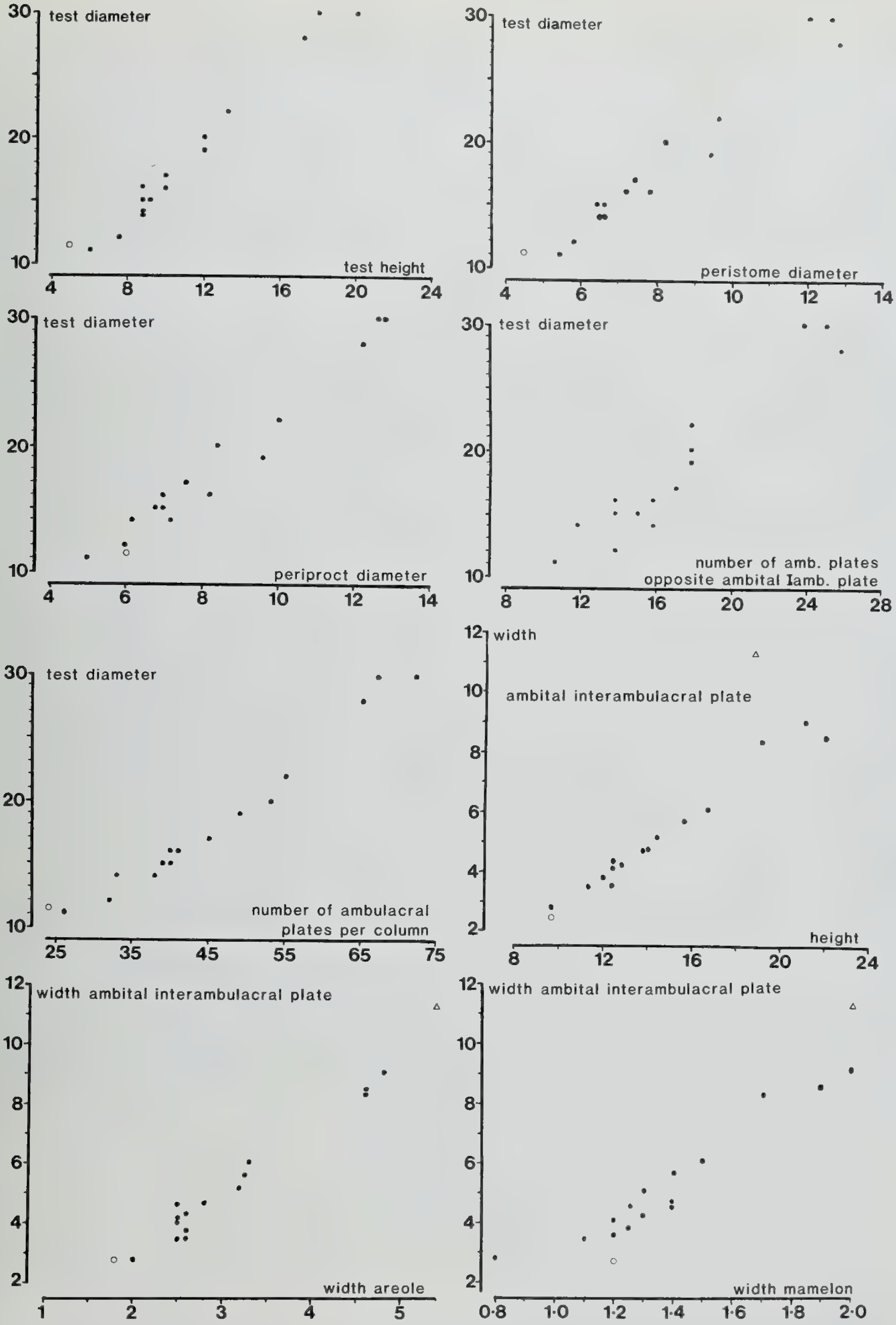


Fig. 13 Biometric data on cidarids: ● = *Stereocidaris uniformis essenensis*, Lower Cenomanian of Wilmington; ○ = *Tylocidaris velifera*, Lower Cenomanian of Warminster; △ = ?*Prionocidaris granulostriata* from the Lower Turonian of Wilmington.

plates must change position relative to the adjacent interambulacral plates, a process that has not previously been recognized.

INTERAMBULACRA. At all sizes, each interambulacral column is composed of just four interambulacral plates with an additional tiny fifth plate adapically in some columns in a proportion of the larger specimens. On all but the most adapical plate in each interambulacrum there is a single large tubercle. These tubercles are not confluent and the mamelon is perforate and surmounts a smooth, non-crenulate platform. The surrounding areole is perfectly circular, moderately sunken and sharply delineated. The scrobicular circle is composed of 12 to 14 small tubercles bordering the areole plus a further 12 or so wedge-shaped tubercles inserted between the first circle but not reaching the border of the areole. The remainder of the plate is covered in densely-packed miliary tubercles. Ambital interambulacral plates have a single row of miliary tubercles on the adradial side of the scrobicular circle, two or three irregular rows on perradial and adoral sides and three to five irregular rows on the adapical side of the scrobicular circle. On adoral plates the rows of miliary tubercles become reduced to just one or two irregular rows. Ambital interambulacral plates are squarish with a width that is, on average, 97% of the height (SD = 7·2; N = 15). The areole forms 53–74% of the plate width (mean = 61%; SD = 7·5; N = 15) and the mamelon is 18–28% of the plate width (mean = 23%; SD = 3·3; N = 15). Adapical plates are taller than ambital plates and the adapical zone of miliary tubercles broadens noticeably. The most adapical plate in each interambulacral zone has only a rudimentary tubercle, a small miliary-free mound, which could not have supported a spine.

PERISTOME. This is circular in outline and almost identical in size to the apical system. In diameter, the peristome is 40–50% of the test diameter (mean = 46%; SD = 3·1; N = 15).

SPINES. A large number of isolated cidarid spines were found at Wilmington, the vast majority belonging to this species. They are stout and cylindrical, up to 2 cm in length and weakly tapered at both ends (Pl. 2, figs 7–8). They are circular in cross section and have a relatively small central mesh zone and an outer cortex. The shaft forms about 80% of the length of the spine and is strongly ribbed. There are approximately 12 vertical ribs around the shaft. Each rib is continuous but scalloped so as to produce a serrated edge. In some of the larger spines small secondary ribs are intercalated between the primary ribs. The distal tip tapers slightly to a blunt point which is often somewhat worn. At the proximal end of the spine there is a smooth, finely-striated neck, a thin milled ring and a conical base. The base has a large central perforation but no crenulate margin.

REMARKS. This species has long been confused with *Cidaris vesiculosa* Goldfuss and it is this name that Wright (1864) used in describing the British material. Schlüter (1892) was the first to realise that two quite different species had been united under this name. One form has sutures that are hardly depressed, fine miliary tuberculation and very fine and dense ambulacral tuberculation; this he referred to *Dorocidaris vesiculosa.* The other has deeply incised sutures, coarser miliary tuberculation and less numerous ambulacral tuberculation and Schlüter placed this in his new species *D. essenensis.* This view was later supported by Lambert (1894). *S. essenensis* differs from *S. uniformis* only in that the oral spines do not have a distally expanded crown. *S. essenensis* is therefore treated as a subspecies of *S. uniformis* Sorignet (1850). A full discussion of this species is to be given by Smith & Wright (in press).

Family **PSYCHOCIDARIDAE** Ikeda, 1936

Genus ***TYLOCIDARIS*** Pomel, 1883

Tylocidaris velifera (Bronn 1835)

Pl. 2, figs 1, 2, 4, 5

1835 *Cidaris velifera* Bronn: 154.
1856 *Cidaris velifera* Bronn; Woodward: 3.
1862 *Cidaris velifera* Bronn; Cotteau (*in* Cotteau 1862–67): 241; pl. 1054, figs 14–21 (see also for earlier references).

1864 *Cidaris velifera* Bronn; Wright: 37; pl. 2, figs 2–4.
1865 *Cidaris velifera* Bronn; Cotteau (*in* Cotteau 1857–78): 59; pl. 2, figs 3–11.
1892 *Tylocidaris velifera* (Bronn) Schlüter: 31; pl. 9, figs 1–7.
1894 *Cidaris velifera* Bronn; Lambert: 40.
1910 *Balanocidaris velifera* (Bronn) Lambert & Thiéry: 146.
1963 *Cidaris velifera* Bronn; Cayeux: 16; fig. 3.

MATERIAL. One incomplete corona of this species (E.81263) was located within the section at Wilmington quarry together with a small number of club-shaped spines (E.81265). Several more spines were collected loose in the quarry but no further specimens of test have been found. The following description is therefore based largely on the well-preserved test figured by Wright (1864: pl. 2, figs 2–3) that came from the Lower Cenomanian of Maiden Bradley, Wiltshire (E.12287).

STRATIGRAPHICAL OCCURRENCE AND DISTRIBUTION. The single specimen of test found at Wilmington came from the very top of the Grizzle, 84 cm below the standard datum level, and therefore from high in the Lower Cenomanian. Stratigraphically located spines were collected within the Grizzle and Wilmington Sands from 271 cm to 641 cm below standard datum level. The other test of *T. velifera* comes from the Lower Cenomanian greensands of Maiden Bradley, Wiltshire.

DESCRIPTION. *SHAPE AND SIZE.* The single whole corona (E.12287) is 11·3 mm in diameter and 5·5 mm in height. The height of the test is 49% of the diameter. In profile, the test is rather flattened compared to most cidarids. The sides are uniformly convex with the ambitus at mid-height, and the oral and apical surfaces are broad and flat.

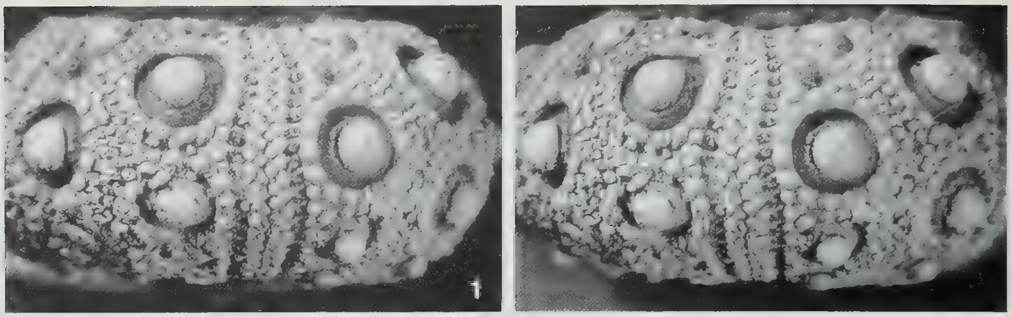
APICAL SYSTEM. Plates of the apical system are not preserved. The apical system is relatively large and very weakly pentagonal in outline. It is 6·0 mm in diameter, which is 53% of the diameter of the test.

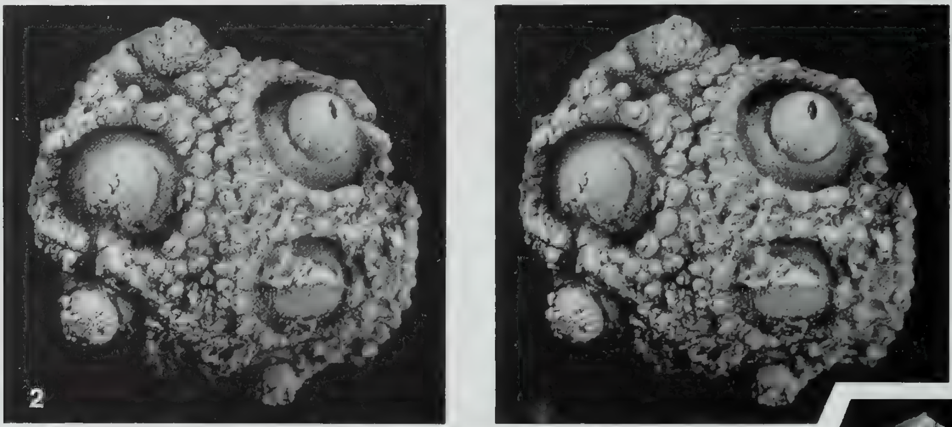
AMBULACRA. These are narrow and slightly sinuous. At the ambitus they are 1·5 mm in breadth, which is 13% of the test diameter. The pores, which are non-conjugate partitioned isopores with a narrow interporal partition, are relatively small and set obliquely. At 11·3 mm test diameter there are 24 ambulacral plates per column. The perradial zone that bears the tubercles is slightly raised and forms 60% of the width of the ambulacral zone of the ambitus. Each ambulacral plate carries a primary tubercle, adjacent to the ambulacral pore, and a rather smaller perradial tubercle offset adorally on the plate. The interporal zone therefore has tubercles that are arranged in a V-shaped pattern, not in horizontal rows as in *Stereocidaris*. At the ambitus there are seven ambulacral plates adjacent to each interambulacral plate.

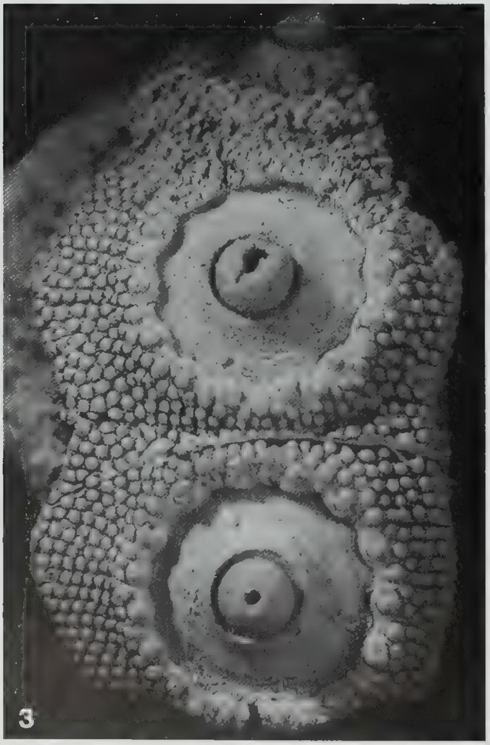
INTERAMBULACRA. There are five plates in each interambulacral column at a test diameter of 11·3 mm. Interambulacral zones at the ambitus measure 42% of the test diameter. Individual plates are slightly broader than they are tall. The Wilmington specimen has ambital interambulacral plates 2·8 mm in breadth and 2·5 mm in height (the plate height is 89% of its breadth). Each plate carries a single primary tubercle. The tubercles at and immediately above the ambitus are noticeably larger than the rest. The mamelon is large (36% of the plate width at the ambitus) and there is a tiny central perforation on ambital and aboral tubercles but not on adoral tubercles. The mamelon covers the upper part of the boss and no platform is developed. The areole is small and circular and is surrounded by a scrobicular circle of about 15 tubercles. Adjacent tubercles are not confluent but adorally and adapically the scrobicular circles of tubercles on neighbouring plates abut. Outside the scrobicular circle there are one or two irregular rows of miliary tubercles, but only on the interradial side of the plate.

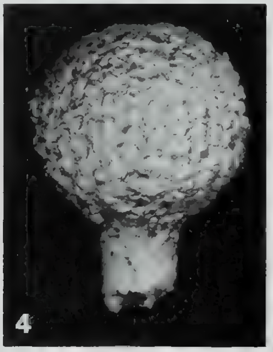
PERISTOME. This is small and circular; at 4·5 mm in diameter it is 40% of the diameter of the test and 75% of the diameter of the apical system.

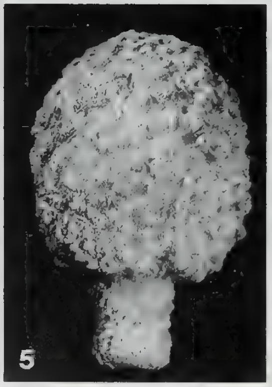
SPINES. The spines of *T. velifera* are small, stout and club-shaped. The shaft may taper down to the base or the transition may be abrupt. Generally, these spines are about half as broad as they are tall and are 7–10 mm in length and 4–5 mm in diameter. The shaft forms about 70% of the length of the spine and is rounded or weakly pointed distally. It is covered in

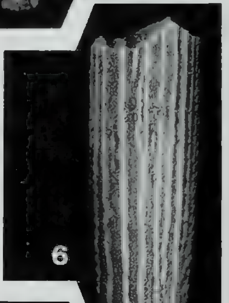

1


2

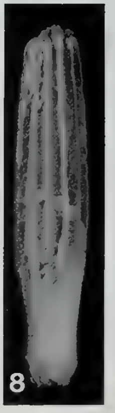

3


4


5


6

7


8

small, stubby thorns that are arranged into 20 to 24 vertical rows. The neck is smooth and there is a thin milled ring and very small base.

Remarks. Originally, this species was erected for club-shaped spines from the Cenomanian of Germany (Bronn 1835). The test remained unknown until Wright (1864) described the specimen from the Lower Cenomanian of Maiden Bradley. *T. velifera* is very similar to the better-known *T. clavigera* König (1825) from the Upper Chalk, the most important difference being that *T. velifera* has perforate tubercles whereas *T. clavigera* has tubercles that are for the most part imperforate. In addition, *T. velifera* has a slightly flatter test and slightly fewer interambulacral plates per column than in *T. clavigera*. Despite these differences, the two species are quite similar and I have chosen to place *T. velifera* in the same genus as *T. clavigera*. The perforations of the mamelon are very small in *T. velifera* and some specimens of *T. clavigera* have perforate adapical tubercles.

Tylocidaris is placed in the family Psychocidaridae by Fell & Pawson (1966).

Genus *PRIONOCIDARIS* Agassiz, 1863

?*Prionocidaris granulostriata* (Desor 1855)

Pl. 2, figs 3, 6

1855 *Cidaris granulostriata* Desor: 14; pl. 5, fig. 26.

One very distinctive fragment of a cidarid test (E.81260), consisting of three interambulacral plates unlike any other, has been found at Wilmington. The largest of the interambulacral plates is 11·3 mm in width and 7·4 mm tall (plate height is 65% of plate width) and is considerably more elongate than plates of *Stereocidaris* or *Tylocidaris*. The mamelon is relatively small, only 1·8 mm in diameter and 16% of the plate width, and has a large central perforation. It is surrounded by a smooth platform and a fairly steep-sided boss. The areole is circular and clearly demarcated, forming 47% of the plate width. It is surrounded by a ring of 15 primary scrobicular tubercles with a further 15 or so smaller scrobicular tubercles inserted between the primary scrobicular tubercles but not in contact with the areole rim. The rest of the plate is covered in densely-packed miliary tubercles, three or four abreast adradially but up to ten abreast perradially. The scrobicular tubercles come close to the edge of the plate both apically and adorally, although adjacent tubercles remain non-confluent and are separated by a single or sometimes a double row of miliary tubercles.

The spines that are found associated at the same level are large, reaching 5 cm in length, and relatively slender, around 6 mm in diameter (Pl. 2, fig. 6). They taper distally to a blunt point and the shaft has about 20 moderately coarse and weakly serrated vertical ribs. Except in size and in the number of ribs, these spines resemble the spines of *Stereocidaris uniformis essenensis*.

The test fragment and spines were collected from the basal glauconitic chalk at Wilmington in the first few centimetres above datum level. They are therefore from the Lower Turonian.

Plate 2

Tylocidaris velifera (Bronn)

Fig. 1 E.12287, lateral. Upper Greensand, Warminster, Wiltshire (× 7).

Fig. 2 E.81262, lateral, interambulacral zone. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 9).

Fig. 4 E.81264, spine. As last (× 4).

Fig. 5 E.81263, spine. As last (× 4·5).

?*Prionocidaris granulostriata* (Desor)

Fig. 3 E.81260, interambulacral plates. Base of the Middle Chalk, Lower Turonian, White Hart sand pit, Wilmington, Devon (× 4·5).

Fig. 6 E.81261, fragment of spine. As last (× 3).

Stereocidaris uniformis essensis (Schlüter)

Fig. 7 E.81336, spine. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 4).

Fig. 8 E.81335, spine. As last (× 3·5).

The gentle curvature of the test fragment suggests that the complete interambulacrum must have been composed of a relatively large number of plates and that the test was fairly tall. The test fragment is identical in all respects with more complete material known from the same horizon on the south Devon coast belonging to the species *Prionocidaris granulostriata* (Desor). A full description of this species is to be given elsewhere (Smith & Wright, in press).

Subclass **EUECHINOIDEA** Bronn, 1860

Infraclass **ACROECHINOIDEA** Smith, 1981

Cohort **ECHINACEA** Claus, 1876

Superorder **STIRODONTA** Jackson, 1912

Order **SALENIOIDA** Delage & Hérouard, 1903

Family **SALENIIDAE** Agassiz, 1838

Genus ***SALENIA*** Gray, 1835

Salenia petalifera Desmarest 1825

Pl. 3, figs 1–4; Figs 14–15

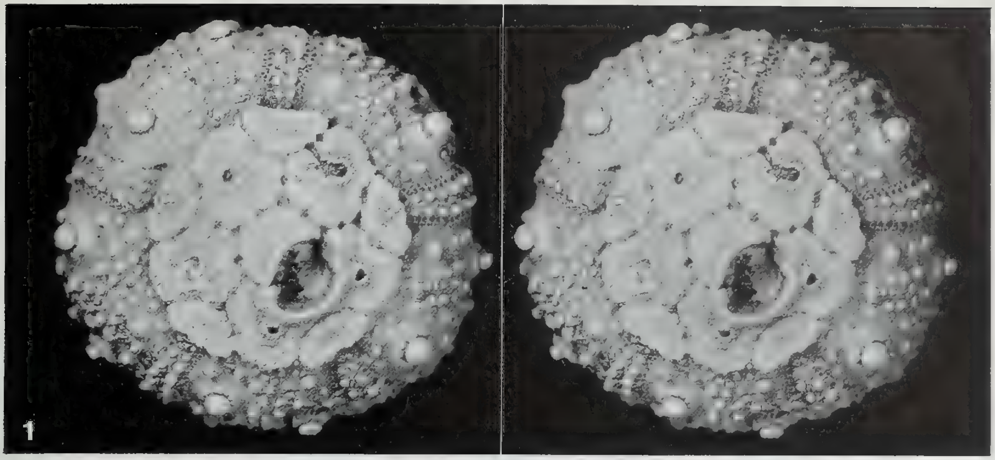
1811 (unnamed) Parkinson: pl. 1, fig. 12.
1825 *Echinus petaliferus* Desmarest: 101.
1838 *Salenia petalifera* (Desmarest) Agassiz: pl. 1, figs 17–24.
1843 *Salenia petalifera* (Desmarest); Morris: 58.
1849 *Salenia personata* Agassiz; Forbes: pl. 5.
1854 *Salenia petalifera* (Desmarest); Morris: 89.
1856 *Salenia petalifera* (Desmarest); Desor: 149; pl. 20, figs 1–3.
1861 *Salenia petalifera* 'Agassiz'; Cotteau: 144; pl. 1034, figs 1–17 (see also for earlier references).
1872 *Salenia petalifera* (Desmarest); Wright: 170; pl. 33, figs 1–4.
1963 *Salenia petalifera* (Desmarest); Cayeux: 19; fig. 7.

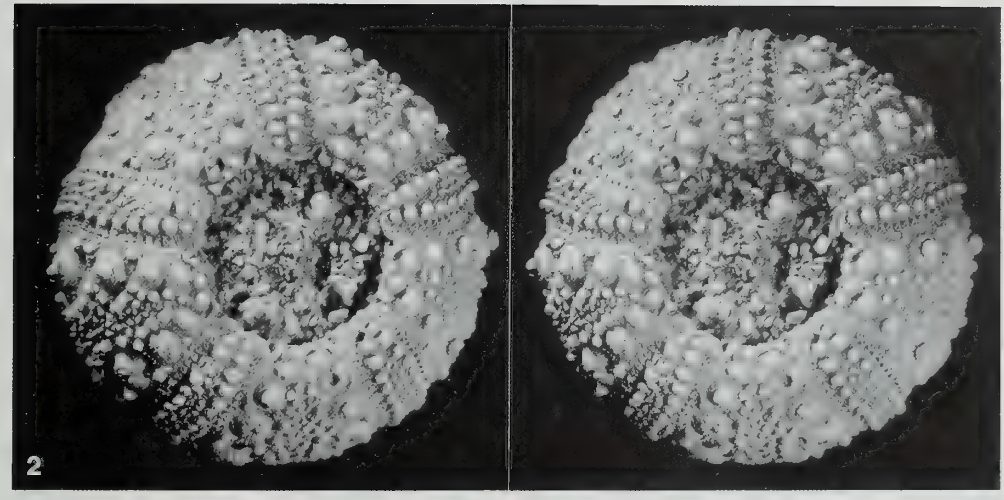
MATERIAL. Twenty-six well-preserved specimens from Wilmington (E.76280–2, E.81173–95) formed the basis of the biometric study. Of these, twelve were accurately located stratigraphically within the succession and the remainder were collected loose on the quarry floor. A further three less well preserved specimens (E.81196–8) have accurate stratigraphical data. In addition, a large number of loose specimens from Wilmington quarry were examined in this study.

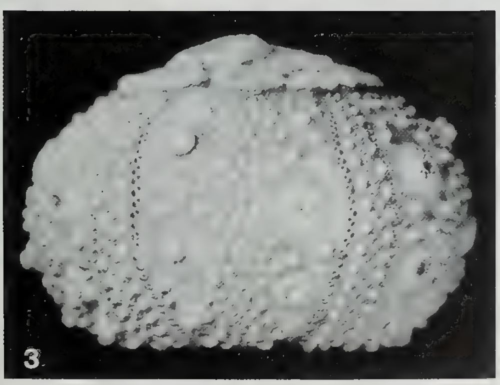
STRATIGRAPHICAL OCCURRENCE AND DISTRIBUTION. At Wilmington, *S. petalifera* is found throughout the Grizzle and the Wilmington Sands, from 84 cm to 773 cm below the standard datum level, in Lower Cenomanian beds. It is a common Cenomanian species also known from the Lower Cenomanian greensands of Wiltshire and the Grey Chalk of Folkstone.

DESCRIPTION. *SHAPE AND SIZE*. The test is circular in outline and ranges from 5·4 mm to 20·3 mm in diameter (mean = 12 mm; SD = 3·8; N = 26). The sides of the test are uniformly rounded and in profile there is a broad flat top and base. The apical system is not quite parallel to the oral surface but slopes gently towards the posterior. The test ranges from 3·0 mm to 13·2 mm in height, 55–76% of the test diameter (mean = 68%; SD = 9·2; N = 26). Smaller individuals are proportionally taller than larger ones.

APICAL SYSTEM. This is large and rather flat, except adjacent to the periproct where there is a prominent spout-like rim. The apical system has a diameter 50–70% of the test diameter (mean = 62%; SD = 4·5; N = 26) and grows isometrically with it (Fig. 14). The periproct is oval, being slightly broader than long, and is bordered by three plates, the large suranal plate and the posterior two genital plates. The periproct is offset towards the posterior right-hand side of the apical disc (Fig. 15) and is elevated above the rest of the apical disc by the spout-like rim developed on the bordering plates. The anterior edge of the periproct lies very slightly posterior to the centre of the apical disc, and the distance from the edge of the apical disc at genital plate 2 to the anterior edge of the periproct is 46–67% of the diameter of the apical disc (mean = 54%; SD = 5·2; N = 26).







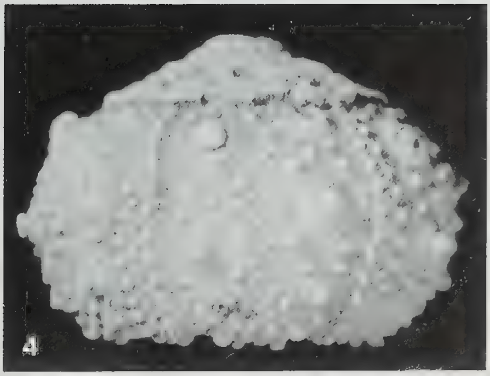


Plate 3
Salenia petalifera (Desmarest)
Fig. 1 E.81174, apical. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 4).
Figs 2, 3 E.76280: 2, oral; 3, lateral. As last (× 4).
Fig. 4 E.81173, lateral. As last (× 5·5).

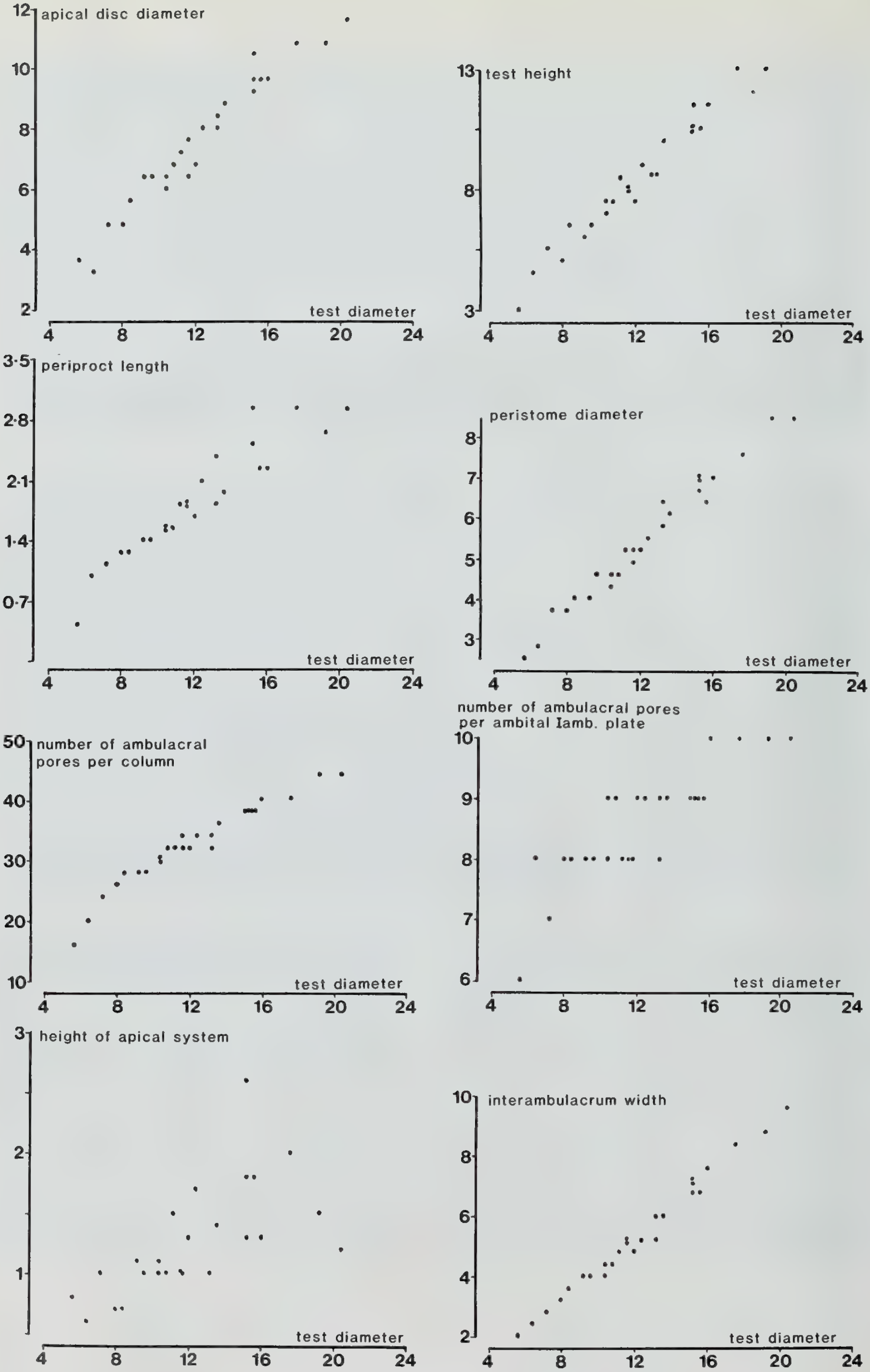


Fig. 14 Biometric data on *Salenia petalifera* from Wilmington.

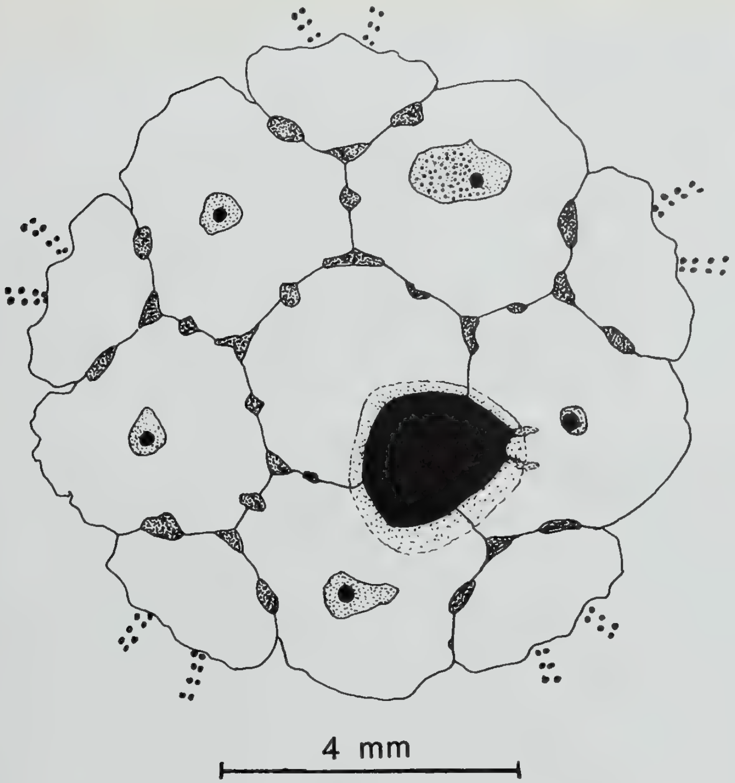


Fig. 15 Camera lucida drawing of the apical disc of *Salenia petalifera* (E.76280), Lower Cenomanian of Wilmington. Ambulacrum III to the top.

All ocular plates are exsert. They are small and triangular, slightly scalloped along their adambital border and with a small median point. No ocular perforation is visible on the upper surface of the ocular plates.

The genital plates are large and are all in contact. The madreporite is the largest of the genital plates and the madreporic perforations for the stone canal are largely hidden and lie within an irregular groove or pit (Fig. 15). Genital pores are more or less centrally placed on the genital plates and are usually surrounded by a small rim; they first appear at a test diameter of about 8 mm. There is a single, large suranal plate in the centre of the apical system.

All plates of the apical system have a weak granular ornamentation. The sutures between ocular and genital plates are ornamented with pits. At each sutural triple junction there is a small pit and further small pits occur midway along each suture (Fig. 15).

AMBULACRA. These are very slightly sinuous adapically but otherwise more or less straight and expand gradually adorally. They are relatively narrow at the ambitus, measuring 13–18% of the test diameter (mean = 15%; SD = 1·2; N = 26). All ambulacral plates are compound with one primary tubercle to every two plates. Ambulacral pores are partitioned isopores throughout and are arranged uniserially, except immediately next to the peristome where the first four to six pores are crowded and have broader muscle-attachment areas. The pore zone forms about 40% of the width of the ambulacral plates at the ambitus. There are 16 ambulacral pores and 8 compound plates in a column at a test diameter of 5·4 mm, rising to 43 ambulacral pores and 21 compound plates at a test diameter of 20·3 mm (Fig. 14). The perradial zone between the columns of pores is raised slightly. Primary ambulacral tubercles are imperforate and are about the same size as interambulacral scrobicular tubercles; they are arranged in a single vertical line in each column. Adorally, the ambulacral tubercles become noticeably larger. As well as the primary ambulacral tubercle, each compound plate has a second, smaller tubercle situated perradially and adorally to the primary tubercle (Pl. 3, figs 3, 4); they are absent in individuals smaller than 7–8 mm in diameter. A further two miliary tubercles may be present above the secondary tubercle in individuals larger than 15 mm test diameter.

INTERAMBULACRA. Interambulacral zones are relatively broad and are 37–48% of the test diameter at the ambitus (mean = 43%; SD = 2·8; N = 26). There are just four interambulacral plates per column at a test diameter of 5·3 mm, five at test diameters of 6·3 mm to about 10 mm, and six in larger individuals. In some of the largest specimens there may be the rudiment of a seventh plate at the apex of one or two columns. Each interambulacral plate has a single primary tubercle, which is ringed by six or seven secondary tubercles. Primary tubercles are largest at and immediately above the ambitus. They are imperforate and crenulate and, in ambital plates, the areole forms on average 71% of the plate width (SD = 8·3; N = 26) and the mamelon 20% of the plate width (SD = 4·4; N = 26). At the ambitus, interambulacral plates are slightly broader than tall, their height being 85–95% of breadth. The secondary tubercles are arranged one at each corner of the plate and midway along the two interradial edges. Interradially, between the rows of secondary tubercles, there is a relatively narrow zone of miliary tubercles. This is broadest at the ambitus, where there may be two or three miliaries abreast, and diminishes both adapically and adorally. The number of ambulacral pores lying adjacent to an ambital interambulacral plate increases from 6 at 5·3 mm test diameter to 10 at 15–20 mm test diameter (Fig. 14).

PERISTOME. This is more or less circular in outline and in diameter 40–52% of the test diameter (mean = 45%; SD = 2·6; N = 26). It is on average 73% of the diameter of the apical system (SD = 6·4; N = 26). Buccal slits are present and are sharply defined but rather shallow (Pl. 3, fig. 2). They have a smooth lip-like rim which extends more or less up to the top of the first interambulacral plate.

REMARKS. This species was first named by Desmarest (1825) in reference to a poor figure given by Parkinson (1811: pl. 1, fig. 12). It was properly described and figured for the first time by Agassiz (1838), and several later workers have given excellent descriptions and figures of this species (Forbes 1849 (as *Salenia personata*), Desor 1856, Cotteau 1861, Wright 1872).

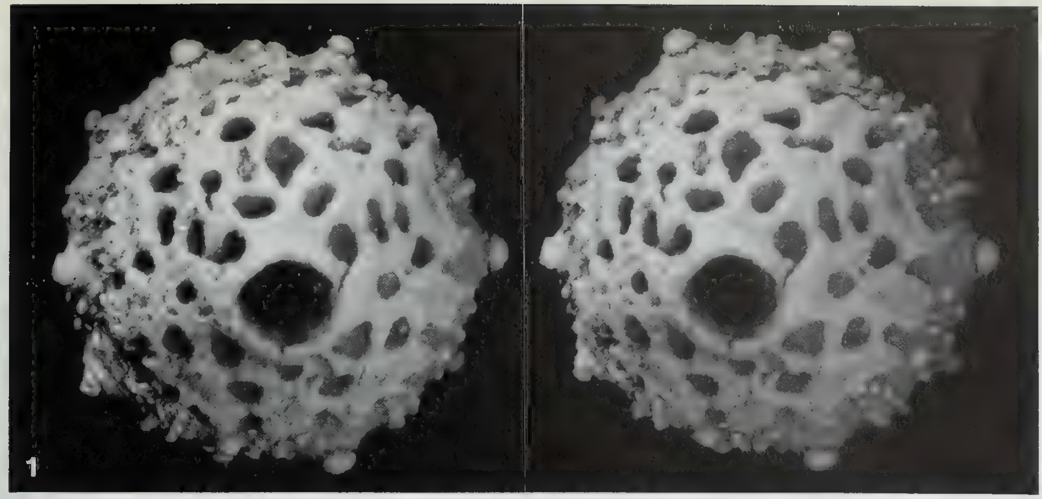
Genus *HYPOSALENIA* Desor, 1856

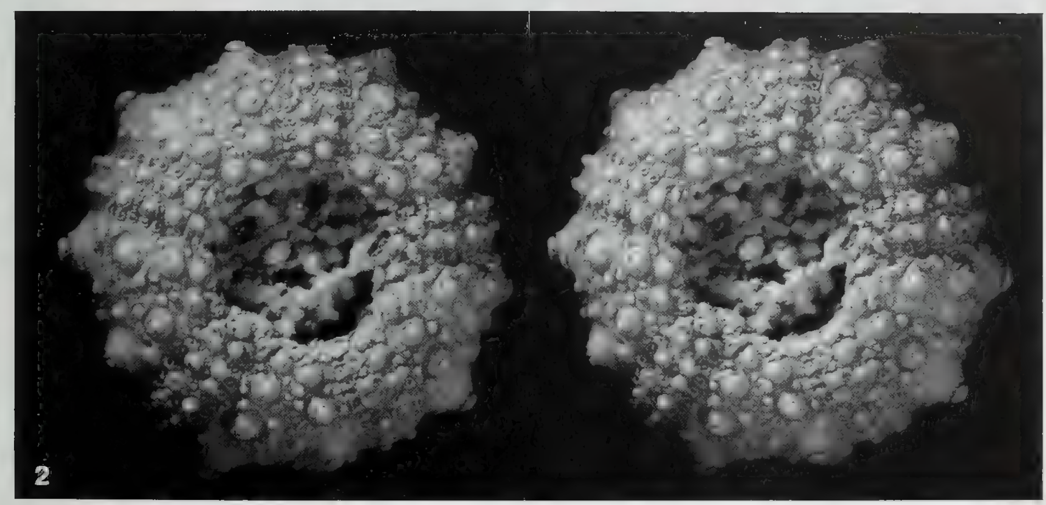
Hyposalenia clathrata (Woodward 1856)

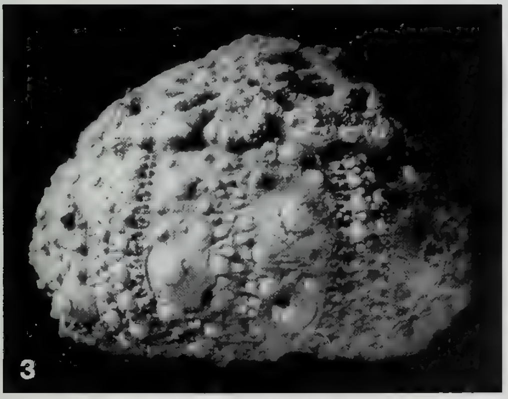
Pl. 4, figs 1–4; Figs 16, 17

?1811 (unnamed) Parkinson: pl. 1, fig. 13.
1843 *Salenia clathrata* Agassiz; Morris: 58 [*nomen nudum*].
1854 *Salenia clathrata* Agassiz; Morris: 89 [*nomen nudum*].
1856 *Salenia clathrata* Agassiz Ms; Woodward: 6 (*partim*).
1856 *Salenia clathrata* Agassiz Ms; Desor: 51.
1861 *Peltastes clathratus* Cotteau (Agassiz); Cotteau: 119 (*partim*); pl. 1028, figs 8–14 [not figs 15–18, = *Hyposalenia umbrella*].
1871 *Peltastes clathratus* (Agassiz); Wright: 156; pl. 32, figs 1–4.
1873 *Peltastes clathratus* (Agassiz); de Loriol: 77; pl. 12, fig. 1.
1892 *Peltastes clathratus* (Agassiz); Schlüter: 148 (*partim*).
1894 *Peltastes clathratus* (Agassiz); Lambert: 44.
1908 *Peltastes clathratus* Cotteau; Valette: 77 (*partim*).
1911 *Peltastes clathratus* (Agassiz); Lambert & Thiéry: 208.
1935 *Hyposalenia clathrata* (Agassiz) Mortensen: 343; fig. 118.
1963 *Hyposalenia clathrata* (Agassiz); Cayeux: 17; fig. 6.
1966 *Hyposalenia clathrata* (Agassiz); Fell & Pawson: U379; fig. 277 1, h.

MATERIAL. The biometric analysis on which the description is based was carried out on 13 specimens from Wilmington (E.81147–59). A large number of specimens from the Cenomanian greensands of Warminster and the Grey Chalk of Dover housed in the British Museum (Natural History) were examined for comparison.


1


2


3

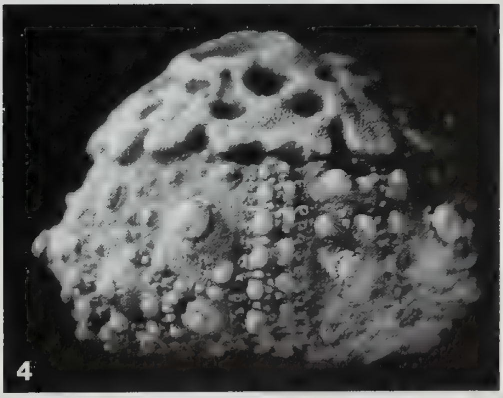
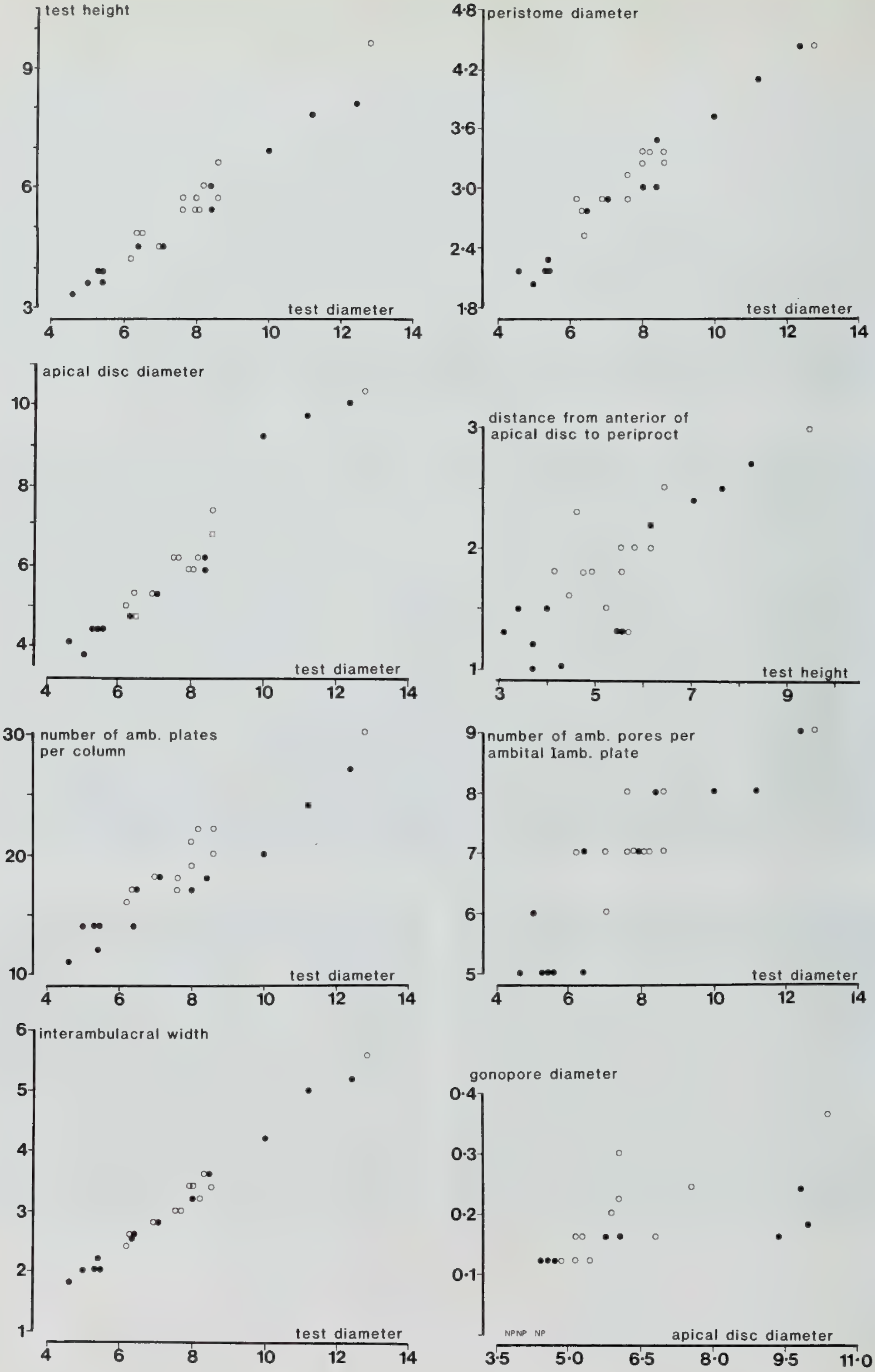

4

Plate 4
Hyposalenia clathrata (Woodward)
Fig. 1 E.81154, apical. Lower Cenomanian, White Hart sand pit, Wilmington, Devon. (× 10).
Fig. 2 E.81147, oral. As last (× 7·5).
Fig. 3 E.81153, lateral. As last (× 8).
Fig. 4 E.81154, lateral. As last (× 10).


test height
9
6
3
test diameter
4
6
8
10
12
14
4·8
peristome diameter
4·2
3·6
3·0
2·4
1·8
test diameter
4
6
8
10
12
14
apical disc diameter
10
8
6
4
test diameter
4
6
8
10
12
14
3
distance from anterior of apical disc to periproct
2
1
test height
3
5
7
9
30
number of amb. plates per column
20
10
test diameter
4
6
8
10
12
14
9
number of amb. pores per ambital Iamb. plate
8
7
6
5
test diameter
4
6
8
10
12
14
6
interambulacral width
5
4
3
2
1
test diameter
4
6
8
10
12
14
gonopore diameter
0·4
0·3
0·2
0·1
NPNP NP
apical disc diameter
3·5
5·0
6·5
8·0
9·5
11·0

Stratigraphical occurrence and distribution. At Wilmington, *H. clathrata* is only present in the Grizzle and was collected from 147 to 257 cm below standard datum, therefore from the Lower Cenomanian. Identical specimens come from the Lower Cenomanian greensands of the Warminster district. Those from the Cenomanian Grey Chalk are, in general, slightly larger with slightly more plates per column than those from Wilmington but are not sufficiently distinct to be separated at species level.

Description. *SIZE AND SHAPE.* The test in profile has a flat base and a moderately conical apical disc. The ambitus is rather low, less than one third of the test height above the base. The base of the apical disc is more or less parallel to the oral surface, but the periproct opens obliquely so as to face slightly towards the posterior. Specimens range from 6·2 to 12·8 mm in test diameter. The test is relatively tall with a height 66–76% of the diameter (mean = 71%; SD = 4·2; N = 13). The apical disc forms 25–50% of the height of the test (mean = 35%; SD = 6·6; N = 13).

APICAL SYSTEM. The apical disc is very large and measures 72–94% of the test diameter (mean = 79%; SD = 4·2; N = 13). It is proportionally larger in smaller individuals. In profile, it is distinctly conical with the periproct immediately to the posterior of the apex. Individual plate sutures are generally rather indistinct and there is a strong ornamentation of deep pits at suture junctions (Fig. 17). The edge of the apical disc is deeply embayed at the sutures between ocular and genital plates.

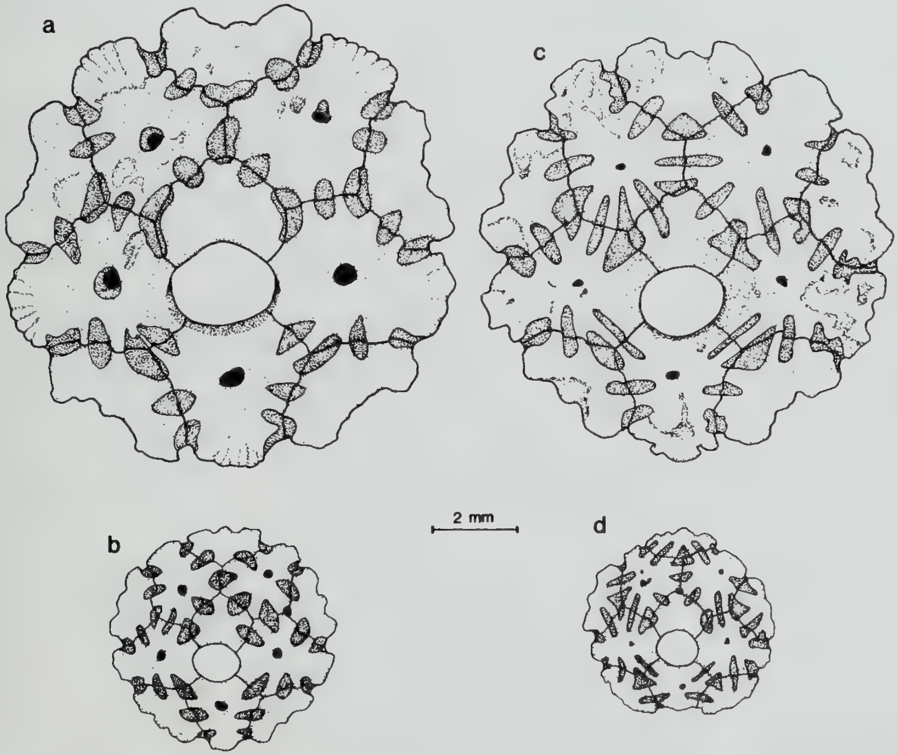


Fig. 17 Camera lucida drawings of the apical discs of adult and juvenile *Hyposalenia clathrata* (a, b) and *H. umbrella* (c, d). a, E.81148; b, E.81155; c, E.81169; d, E.81165.

Fig. 16 Biometric data on *Hyposalenia clathrata* (○) and *Hyposalenia umbrella* (●) from the Lower Cenomanian of Wilmington. NP = gonopores not present.

Ocular plates are triangular in outline in juveniles but become broadly crescentic in larger individuals, with the development of a perradial concavity at their outer edge. The ocular pore is hidden from above. Genital plates are almost trapezoidal in outline, tapering adambitally, and with a gonopore situated slightly off-centre towards the inner edge of the plate. No madreporic perforations were apparent on any specimen. The centre of the apical disc is occupied by a relatively small, pentagonal suranal plate.

Apical plates are often covered in light irregular pittings while distally on genital plates sometimes feeble radial ridges and grooves are developed. The deep pits which give the apical disc its characteristic ornamentation are located at points where three plate sutures meet and mid-length along suture between two adjacent plates (Fig. 17a, b). This is precisely the same position as pits in *H. umbrella* and *Salenia petalifera* (see Figs 17c, d and 15). These pits are large and ovoid in outline. Gonopores first appear in genital plates at about 6 mm test diameter and are a little larger than those of *H. umbrella* at a corresponding size (Fig. 16).

The periproct is relatively small and oval in outline. It is 15–19% of the test diameter in length (mean = 22%; SD = 6·6; N = 12), and is bordered by genital plates 1, 4 and 5 and the suranal plate. It is very slightly broader than long and in adults the apical system is drawn out as a weak spout surrounding the periproct. The anterior lip of the periproct forms the tallest point on the test and the periproct opening slopes slightly backwards to face posteriorly. The anterior edge of the periproct lies 45–60% of the distance from the anterior edge to the posterior edge of the apical disc (mean = 53%; SD = 5·5; N = 12).

PERISTOME. This is relatively small, 35–46% of the test diameter (mean = 40%; SD = 3·1; N = 12), and circular in outline. The oral surface is rather flat and the peristome very slightly sunken. There are small but sharply-defined buccal slits.

AMBULACRA. These are more or less straight and maintain approximately the same width along most of their length. At the ambitus ambulacra are 21–36% of the interambulacral width (mean = 30%; SD = 3·5; N = 12). All ambulacral plates are compound in a bigeminate diadematoid style. The ambulacral pores are arranged as a single linear series, without any crowding adorally. They are all partitioned isopores corresponding to types P_1 and P_2 of Smith (1978). The pore zone forms about 35–40% of the ambulacral plate width and the raised perradial zone of tubercles occupies 60–65% of the width of the ambulacral zone at the ambitus. The number of ambulacral plates in a column increases from 16 at 6·5 mm test diameter to 30 at 12·8 mm test diameter (Fig. 16). Each compound plate bears a single primary tubercle straddling the two individual plates. These are about the same size as scrobicular tubercles on interambulacral plates and do not become noticeably enlarged adorally. Between successive primary tubercles in one column there is a row of two or three miliary tubercles, while perradially there are also miliary tubercles, one or two abreast, arranged so as to form a somewhat zig-zag perradial zone of granules between the two rows of primary ambulacral tubercles (Pl. 4, figs 3, 4). In small specimens there are only three or four ambulacral plates opposite each ambital interambulacral plate, but this rises to seven or eight in larger specimens (Fig. 16).

INTERAMBULACRA. Interambulacral zones are relatively broad (39–43% of the test diameter, mean = 40%; SD = 1·4; N = 13). They taper quite markedly adorally, but only slightly adapically. There are only 3–4 plates per column in small individuals, rising to five, with or without a rudimentary sixth plate in some columns in specimens of about 7 mm in diameter or over. Ambital plates are pentagonal and approximately as tall as they are wide. Each plate has a single primary tubercle and there is only one large tubercle per column, either at or slightly above the ambitus. More adapical tubercles are generally rudimentary while subambital tubercles are very much smaller, though fully formed. The mamelon is about 20% of the plate width (SD = 3·5; N = 13) while the areole is 68–90% of the plate width (mean = 76%; SD = 2·3; N = 13). The mamelon is imperforate and surmounts a crenulate platform which has 11 or 12 crenulae. Tubercles are not confluent. Five or six much smaller secondary tubercles surround each primary tubercle forming a widely-spaced scrobicular circle. They are situated one at each angle of the plate with the sixth midway along the upper interradial plate margin. Along the interradial plate margin there are generally a number of still smaller miliary tubercles, but this zone is narrow and there are never more than two or three miliaries abreast in this region.

Remarks. There has been some disagreement as to whether *Hyposalenia clathrata* and *H. umbrella* are distinct species. Agassiz (*in* Morris, 1843) was the first worker to distinguish these two forms, giving them their specific names. However, *H. clathrata* did not become a valid species until 1856 when Woodward gave a description of it. In this Woodward suggested that *H. umbrella* was merely a variety of *H. clathrata.* Cotteau (1861) provided excellent figures of both species and claimed to have specimens that showed a range of intermediates between the two forms. T. Wright (1871), however, chose to maintain the two species and provided the first valid description of *H. umbrella.* Since then Szorenyi (1955) and C. W. Wright (1967) have both maintained *H. clathrata* and *H. umbrella* as distinct species.

The two forms at Wilmington are distinguished on the basis of apical disc ornamentation. In *H. clathrata* the apical disc has large oval pits, whereas in *H. umbrella* they take the form of elongate slits and triangular pits (Figs 17a, b and c, d). Although there is a small amount of variation in the size and pattern of these sutural pits, the two forms at Wilmington are easy to distinguish. The biometric study of the Wilmington fauna confirms the observations of T. Wright (1871) and C. W. Wright (1967) that in other respects the two forms seemed to be identical. One slight difference that was noticed was that *H. clathrata* appeared to have slightly more ambulacral plates per column at all sizes (Fig. 16).

Stratigraphically, however, the two forms do not occur together. *H. clathrata* is found between 250 and 150 cm below datum level whereas *H. umbrella* is found both immediately above in the top part of the Grizzle as well as in the lower part of the Wilmington Sands. The level at which *H. clathrata* is replaced by *H. umbrella* is also where *Cottaldia granulosa* is replaced by *C. benettiae.*

There are, however, significant differences in the size of the gonopores in the two forms. Gonopores of *H. clathrata* are usually somewhat larger than those of *H. umbrella* (Fig. 16). A regression analysis of gonopore diameter (x) against test diameter (y) gives the following equations:

$$\begin{aligned} &H.\ clathrata\text{:} \quad x = -8{\cdot}72 + 2{\cdot}11y\ (R^2 = 75\%) \\ &H.\ umbrella\text{:} \quad x = -7{\cdot}46 + 2{\cdot}65y\ (R^2 = 55\%) \end{aligned}$$

Differences in gonopore size are usually associated with sexual dimorphism (Kier 1967, Smith 1984), females having larger gonopores than males. This occurs only in those species where larval development is foreshortened and the females produce large, yolk-rich eggs. Usually in such cases the females will brood their young and have specially modified pouches (see Philip & Foster 1971, Roman 1983).

It is therefore possible that, because the two forms differ only in the size and shape of apical pitting and the development of gonopores, they could represent males and females of the same species. *H. clathrata*, with larger gonopores and oval sutural pits possibly for brooding, would then be female while *H. umbrella* with narrower slit-like pores and smaller gonopores would be male. As against this, the non-overlapping occurrence of the two forms suggests that they represent two discrete populations living contemporaneously and separated from one another either geographically or ecologically. They presumably replaced one another as local conditions changed.

Hyposalenia umbrella (Wright 1871)

Pl. 5, figs 1–3; Figs 16, 17

1843 *Salenia umbrella* Agassiz Ms; Morris: 58 [*nomen nudum*].
1854 *Salenia umbrella* Agassiz Ms; Morris: 89 [*nomen nudum*].
1856 *Salenia umbrella* Agassiz Ms; Woodward: 6 [*nomen nudum*].
1861 *Peltastes clathratus* Cotteau (Agassiz); Cotteau: 119 [*partim*]; pl. 1028, figs 15–18 only.
1871 *Peltastes umbrella* (Agassiz Ms); Wright: 158; pl. 34, figs 1–3.
1911 *Peltastes umbrella* '(Agassiz)'; Lambert & Thiéry: 208.
1955 *Hyposalenia umbrella* (Wright); Szörényi: 15; pl. 1, figs 1–4; text-fig. 1.

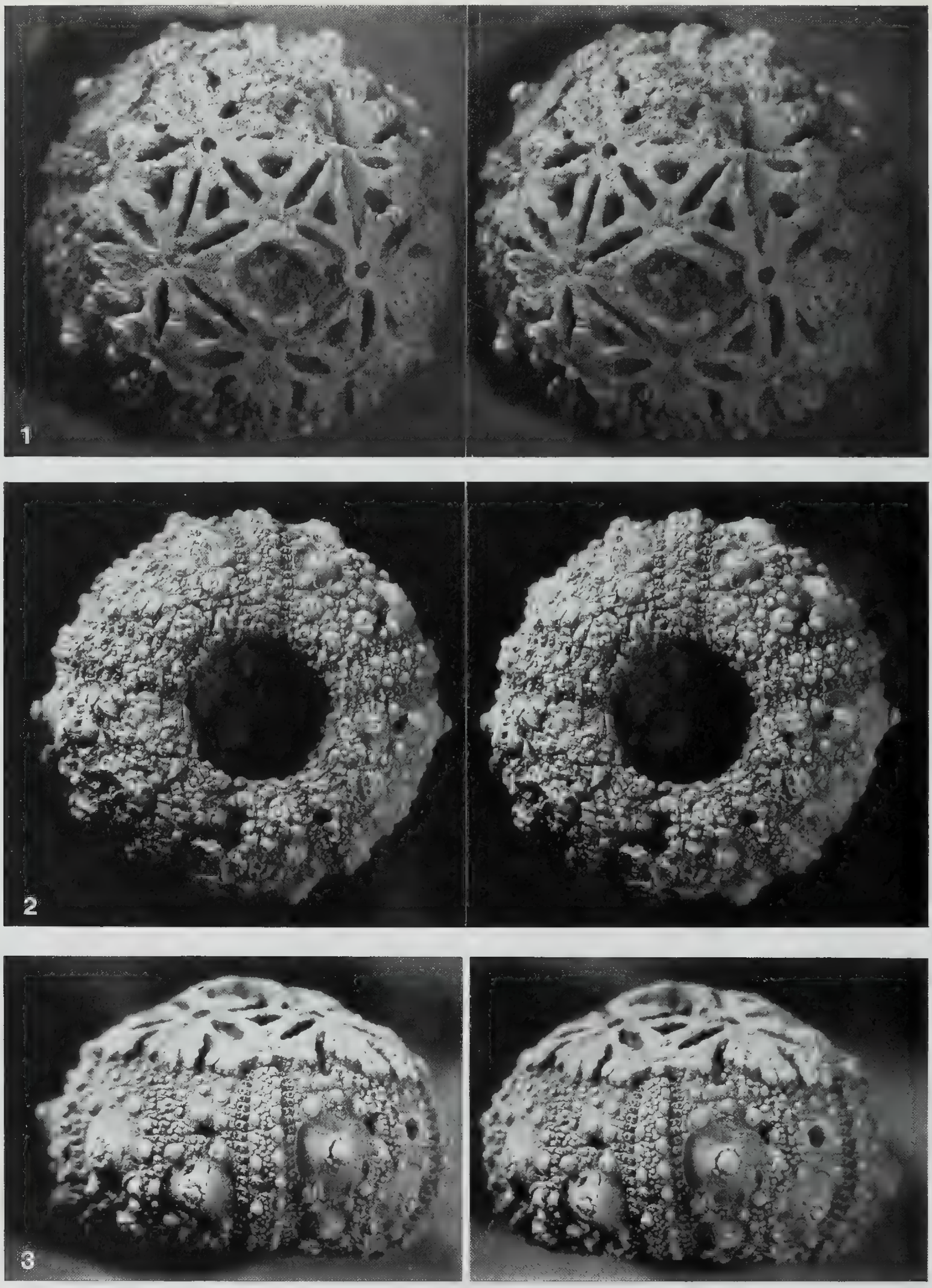


Plate 5
Hyposalenia umbrella (Wright)
Figs 1–3 E.81168: 1, apical; 2, oral; 3, lateral. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 5·5).

Material. Twelve well-preserved specimens from Wilmington were used in the biometric analysis (E.81160–71). Further material of this species from the Cenomanian greensands of Warminster and the Grey Chalk of Folkstone housed in the British Museum (Natural History) was also examined for comparison. This included the type specimen E.12554, from the Warminster Greensands, studied by Agassiz and figured and described by Wright (1871: pl. 34, fig. 1).

Stratigraphical occurrence and distribution. At Wilmington *H. umbrella* was found towards the top of the Grizzle, at 134 and 104 cm below standard datum, and towards the base of the Wilmington Sands at 774 and 880 cm below standard datum. It therefore belongs to the Lower Cenomanian. Like *H. clathrata*, the population of *H. umbrella* from the Grey Chalk at Folkestone are, in general, slightly larger with more plates per column than either of the populations from Wilmington or Warminster.

Description. *SIZE AND SHAPE.* Specimens range in size from 4·6 to 12·4 mm in test diameter. Test height is 65–74% of the diameter (mean = 69%; SD = 2·5; N = 12) and the apical disc forms 23–48% of the test height. Test shape is more or less identical to that of *H. clathrata.*

APICAL SYSTEM. The apical disc is very large and measures 73–94% of the test diameter (mean = 80%; SD = 6·8; N = 12). It is proportionally larger in juveniles. In its shape and plate arrangement it is identical to that of *H. clathrata* (see p. 51), differing only in the slightly smaller size of the gonopores (Fig. 16), and in the shape of the sutural pits. In *H. umbrella* these are narrow and slit-like or triangular (Fig. 17c, d).

PERISTOME. This is 36–42% of the test diameter in size (mean = 40%; SD = 3·1; N = 12). It is circular in outline, slightly sunken and has small but sharply-defined gill slits.

AMBULACRAL AND INTERAMBULACRAL ZONES. These are identical to those of *H. clathrata* (see p. 52).

Remarks. The reasons for maintaining *H. umbrella* as a discrete species distinct from *H. clathrata* are outlined in the discussion of the latter. Although the name *umbrella* was first coined by Agassiz for a specimen in the British Museum (Natural History), the name was not validated until Wright (1871) described and figured Agassiz' specimen.

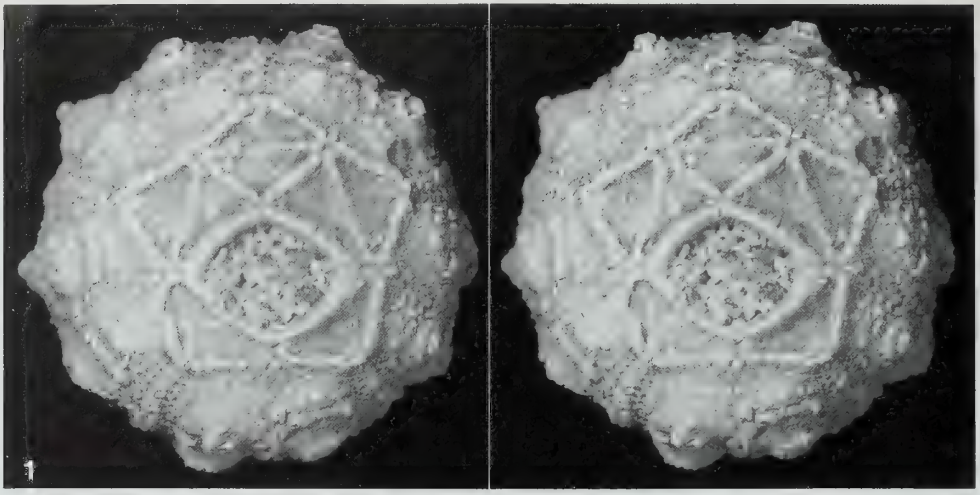
Genus ***GONIOPHORUS*** Agassiz, 1838

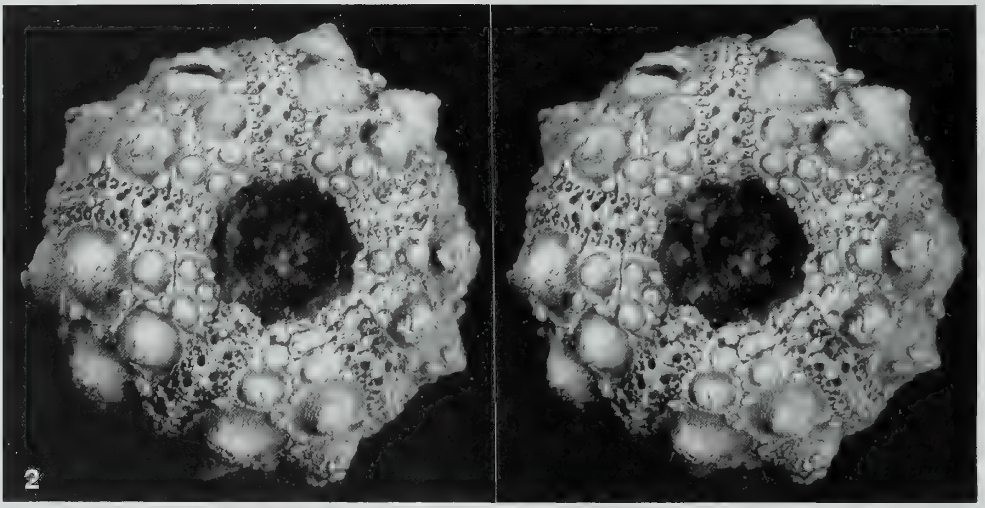
Goniophorus lunulatus Agassiz 1838
Pl. 6, figs 1–4; Figs 18, 19

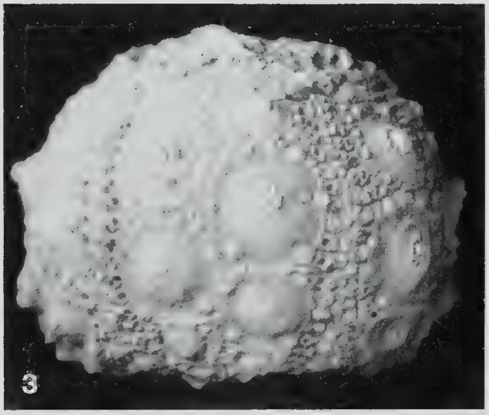
1838 *Goniophorus lunulatus* Agassiz: 30; pl. 5, figs 17–24.
1838 *Goniophorus apiculatus* Agassiz: 32; pl. 5, figs 25–32.
1843 *Goniophorus favosus* (Ag. Ms); Morris: 52.
1843 *Goniophorus lunulatus* Agassiz; Morris: 52.
1854 *Salenia lunulata* (Agassiz) Morris: 89.
1861 *Goniophorus lunulatus* Agassiz; Cotteau: 126; pl. 1029, figs 8–19.
1872 *Goniophorus lunulatus* Agassiz; Wright: 166; pl. 36, figs 1, 2.
1892 *Goniophorus lunulatus* Agassiz; Schlüter: 155.
1911 *Goniophorus lunulatus* Agassiz; Lambert & Thiéry: 209.
1911 *Goniophorus apiculatus* Agassiz; Lambert & Thiéry: 210.
1935 *Goniophorus lunulatus* Agassiz; Mortensen: 346; fig. 191.
1955 *Goniophorus lunulatus* Agassiz; Szörényi: 17; pl. 1, figs 10–14; text-figs 2–5.
1966 *Goniophorus lunulatus* Agassiz; Fell & Pawson: U380; fig. 279.1.

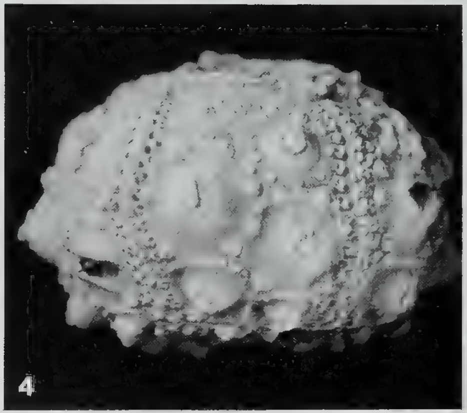
Material. Eighteen whole tests (E.81125–43) collected from the quarry at Wilmington were used in the biometric study of this species; five of these are located accurately within the stratigraphical succession. A further three specimens, less well preserved, also have accurate stratigraphical data. Specimens from the Lower Cenomanian greensand of Warminster were also examined.

Stratigraphical occurrence and distribution. The species is very well known from the Cenomanian of Wiltshire and France. At Wilmington, *G. lunulatus* is found in the Grizzle and


1


2


3


4

the Wilmington Sands, from 117 cm to 598 cm below the standard datum level and is most common in the Grizzle (Fig. 7). Here it comes from the Lower Cenomanian.

DESCRIPTION. *SHAPE AND SIZE.* The test is circular in outline with steep, uniformly curved sides and a flat top and base. Specimens range in size from 4·0 to 10·7 mm in diameter (mean = 7 mm; SD = 1·8; N = 18) and from 3·0 to 7·6 mm in height. Test height is 63–86% of the diameter (mean = 73%; SD = 6·0; N = 17). The apical system is generally flat, but in some specimens it is conical and forms about 11% of the total height of the test. The peristome is only very slightly sunken.

APICAL SYSTEM. This is relatively large and approximately pentagonal in outline. In length it is 46–73% of the test diameter (mean = 65%; SD = 7·8; N = 17). The periproct is oval or diamond-shaped in outline, and is slightly broader than long. The length of the periproct is on average 83% of the breadth (SD = 6·2; N = 16). It lies on the anterior–posterior axis, slightly posterior to the midpoint, so that the distance from the anterior edge of the apical system to the anterior edge of the periproct is on average 48% of the diameter of the apical disc (SD = 4·2; N = 16). The periproct is relatively small and measures only 21–30% of the test diameter (mean = 25%; SD = 2·4; N = 16). It is surrounded by a prominent rim. Four plates border the periproct (Fig. 19), genital plates 1, 4 and 5 and the single suranal plate. The ocular plates are all exsert, roughly diamond-shaped and without obvious ocular pore. The genital plates are all of similar size and each has a single gonopore situated centrally. The relatively small suranal plate is pentagonal and is broader than long.

In profile, the anterior edge of the periproct forms the highest part of the test so that the periproct opening is inclined slightly towards the posterior. The apical system is ornamented with ridges in a very characteristic arrangement (Fig. 19). Ridges radiate from the region of each gonopore to the point of each ocular, to the angles of the periproct and to adjacent gonopores. Both the outer ridge (that joining the points of the oculars) and the rim around the periproct are sharply delineated, accentuating the pentagonal outline of the apical system. The gonopores appear in genital plates at test diameters of about 5 or 6 mm.

AMBULACRA. These are almost straight, becoming very slightly sinuous in only the largest specimens. Ambulacral plating is simple at the ambitus and adapically, but is bigeminous adorally where the primary ambulacral tubercles are noticeably larger and overlap two plates each. There are 12–13 plates in an ambulacral column at 4 mm test diameter, rising to 27 plates at 10 mm test diameter (Fig. 18). In a single ambulacral column, only the eight most adoral plates are fused to form four compound plates. The ambulacra are extremely narrow and, at the ambitus, measure only 9–14% of the test diameter (mean = 12%; SD = 1·2; N = 18).

Ambulacral pores are all partitioned isopores with only narrow muscle-attachment zones. They are arranged uniserially down to the peristome, with no hint of phyllode development, and are set slightly obliquely. Succeeding pores are widely spaced. The pore zone is relatively broad, so that the raised perradial track between the pore zones is just a little less than half of the ambulacral width (mean = 43%; SD = 5·1; N = 18). Each ambulacral plate from the ambitus adapically carries a single primary tubercle. In this region the perradial zone between the columns of ambulacral pores is extremely narrow and there is only space for primary ambulacral tubercles (Pl. 6, fig. 3). Subambitally, between the larger primary tubercles, there are three or four deep pits, presumably for sphaeridia, in each column (Pl. 6, fig. 2).

INTERAMBULACRA. Interambulacral zones are 35–45% of the test diameter in width at the ambitus (mean = 41%; SD = 2·6; N = 18). They taper slightly adapically, but very strongly adorally where they are only half the width that they attain at their adapical end. They are about 3·5 times the width of ambulacral zones at the ambitus. There are 4–5 interambulacral

---

Plate 6

Goniphorus lunulatus Agassiz

Fig. 1 E.81126, apical. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 7).

Figs 2, 4 E.81139: 2, oral; 4, lateral. As last (× 7).

Fig. 3 E.81140, lateral. As last (× 8).

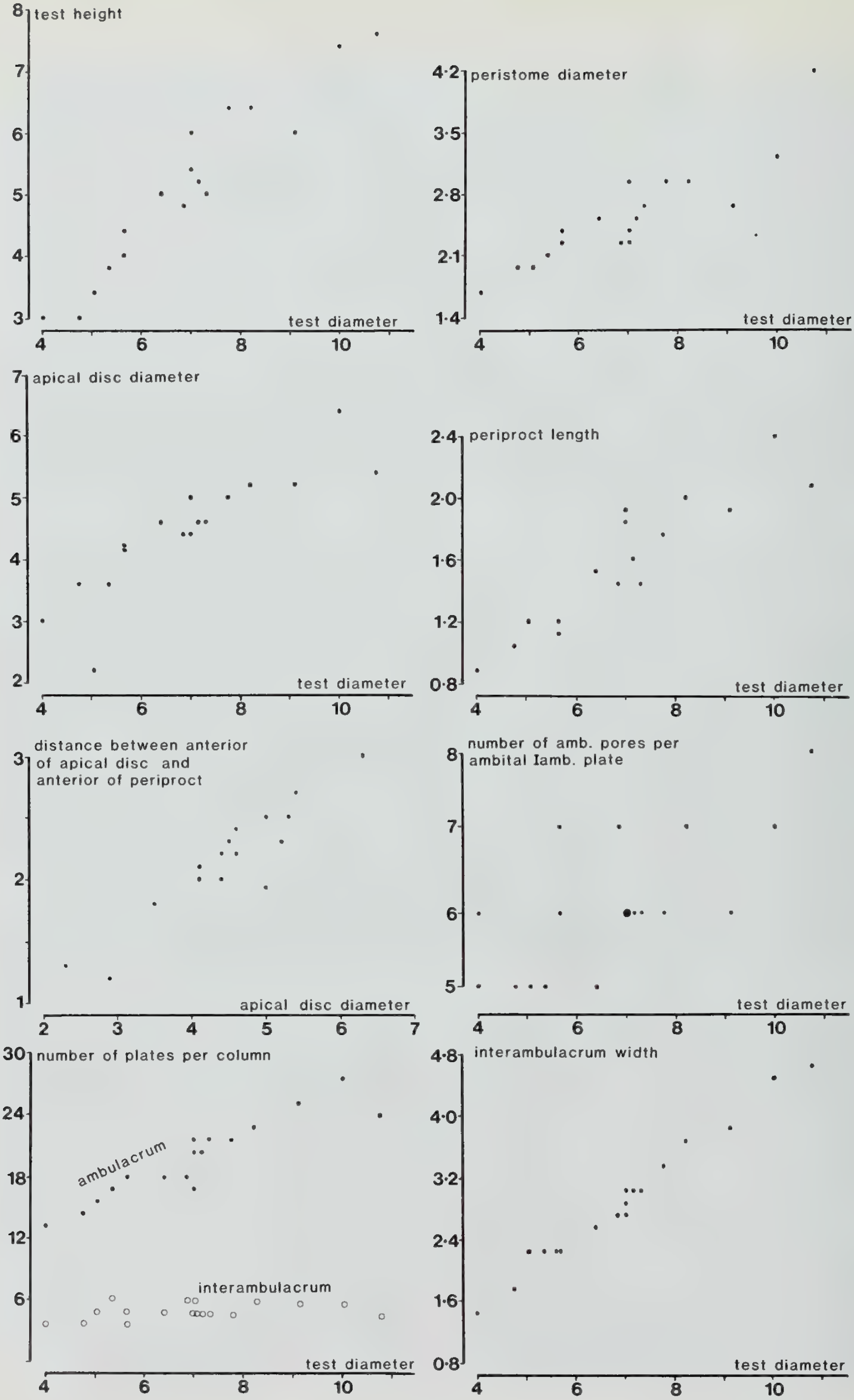


Fig. 18 Biometric data on *Goniophorus lunulatus* from the Lower Cenomanian at Wilmington.

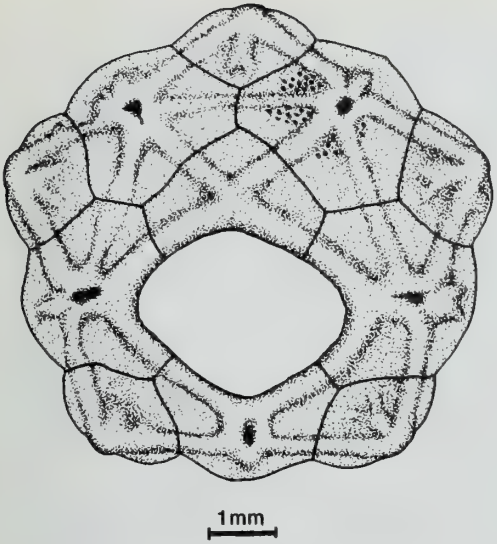


Fig. 19 Camera lucida drawing of the apical disc of *Goniophorus lunulatus* (E.81125) from Wilmington. Ocular III to the top.

plates per column at 4 mm test diameter, and 5–6 plates from 6 to 10 mm test diameter. All interambulacral plates have a single large tubercle and plate height and plate width are more or less equal at the ambitus (height is on average 98% of the width; SD = 0·05; N = 18). The primary tubercle occupies most of each plate and is surrounded by a narrow circle of generally five small secondary tubercles, which are arranged in such a way that those on adjacent plates alternate, forming a more or less continuous zig-zag row interradially (Pl. 6, fig. 3). Adorally, the secondary tubercles become arranged into two discrete rows but never have miliary tubercles between the rows. The areole is circular and forms about 80% of the plate width ambitally. The boss is tall and steep-sided, and is surmounted by a very small, imperforate tubercle that is only about 16% of the plate width (SD = 2·7; N = 18). Tubercles are weakly crenulate. There are 5–6 ambulacral pores adjacent to ambital interambulacral plates in small individuals and 6–7 in larger specimens.

PERISTOME. This is small and circular in outline, and only very slightly sunken. In diameter it is 30–43% of the test diameter (mean = 37%; SD = 3·8; N = 18). Buccal slits are present, although fairly small, and are bounded by a sharp rim.

REMARKS. This very distinctive species was properly described and figured by Agassiz (1838) and there has been little taxonomic confusion over it. Although previous authors have suggested that its ambulacral pores were simple throughout, the most adoral plates are undoubtedly bigeminate. Each pair of plates has a single large primary tubercle and, adorally, a deep, circular sphaeridial pit. The circular pits are better developed in this species than in any other saleniid I have seen. The apical disc figured by Wright (1872: pl. 36, fig. 2) is rather unusual in that it lacks the less well developed ridges that run between adjacent gonopores. The figure given here (Fig. 19) is much more typical of the species, from both Wilmington and Warminster.

Family **PSEUDODIADEMATIDAE** Pomel, 1883

Genus ***TIAROMMA*** Pomel, 1883

Tiaromma michelini (Agassiz, *in* Agassiz & Desor 1847)

Pl. 7, figs 1–4; Fig. 20.

1840*b* *Diadema Michelini* Agassiz: 8 [*nomen nudum*].
1843 *Diadema ornatum* Woodward, *in* Morris: 51 (*non* Goldfuss).

1847 *Diadema Michelini* Agassiz; Agassiz & Desor: 43.
1854 *Diadema Benettiae* Forbes, *in* Morris: 76 [*nomen nudum*].
1854 *Diadema ornatum* Forbes, *in* Morris: 77 (*non* Goldfuss).
1856 *Diadema ornatum* Woodward: 6 (*non* Goldfuss).
1856 *Diadema Benettiae* Forbes; Woodward: 7.
1858 *Diadema Michelini* Agassiz; Desor: 72.
1858 *Diadema Benettiae* Forbes; Desor: 72.
1864 *Pseudodiadema Michelini* (Desor) Cotteau: 476; pl. 1114, figs 1–13 (see also for earlier European records).
1864 *Pseudodiadema ornatum* Cotteau: 480; pl. 1115, figs 1–12 (*non* Goldfuss).
1867 *Pseudodiadema Benettiae* (Forbes) Wright: 101; pl. 15, fig. 2.
1867 *Pseudodiadema ornatum* Wright: 103; pl. 16, fig. 4; pl. 19, fig. 1; pl. 21, figs 1, 2 and pl. 21a, fig. 1 (*non* Goldfuss).
non 1867 *Pseudodiadema Michelini* Wright: 99; pl. 19, fig. 2 [= *Polydiadema bonei* (Forbes)].

Material examined. As well as a plaster cast of Agassiz' holotype housed in the British Museum (Natural History), I have examined the type series of *Diadema benettiae* Forbes (Geological Survey Museum, IGS 40308–17) and the specimens of this species figured by Wright (1867) (E.1601 and E.12548). About 60 specimens were collected from the White Hart Pit at Wilmington, of which 27 well-preserved specimens (E.76283, E.80066–90) were used in the biometric analysis. Twenty-six specimens were accurately located within the stratigraphical succession. For comparison, a large number of specimens from the Cenomanian Grey Chalk of Dover, identified by Wright as *Pseudodiadema ornatum*, were also studied.

Stratigraphical occurrence and distribution. At Wilmington, this species was collected from the Grizzle and the Wilmington Sands, from 184 cm to 825 cm below standard datum level. It is particularly common between 270 and 400 cm below standard datum, around the junction between the Grizzle and the Wilmington Sand. Elsewhere in Britain *T. michelini* is found in the Lower Cenomanian greensands of Warminster and Cambridge, the Middle Cenomanian Chlorite Marl near Chard, Somerset, the Grey Chalk of the Folkestone Region, and from the *dispar* Zone (Albian) of Dorset.

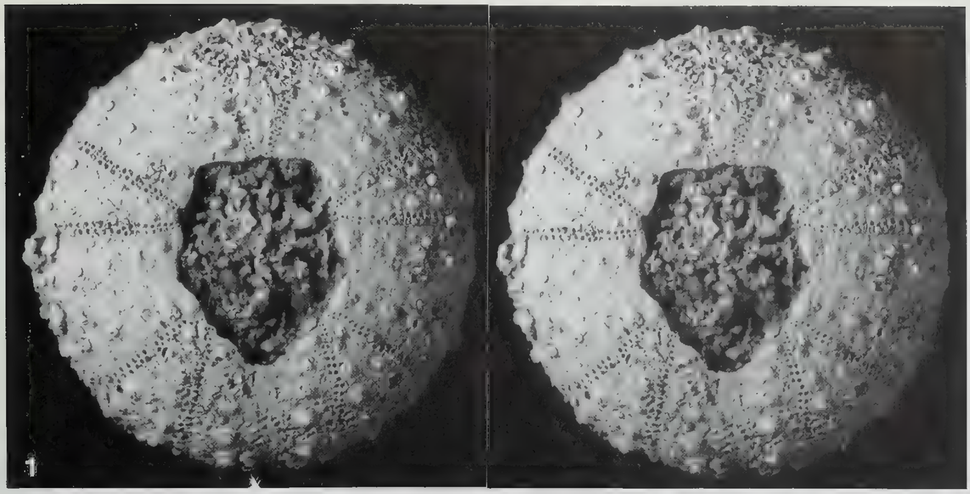
Description. *SHAPE AND SIZE.* Specimens range in size from 9·3 to 31·1 mm in diameter (mean = 18·5 mm; SD = 5·21; N = 27) and are circular in outline. There is quite a wide variation in test height (Fig. 20), which ranges from 36–52% of the test diameter (mean = 46%; SD = 3·0; N = 27). In profile, the test is rather inflated with broad, flat oral and apical surfaces. The sides are uniformly curved and the ambitus is at mid-height. Juveniles of *T. michelini* are relatively easy to distinguish from other juvenile pseudodiadematids because of their tumid profile and the small size and sparseness of their primary tuberculation.

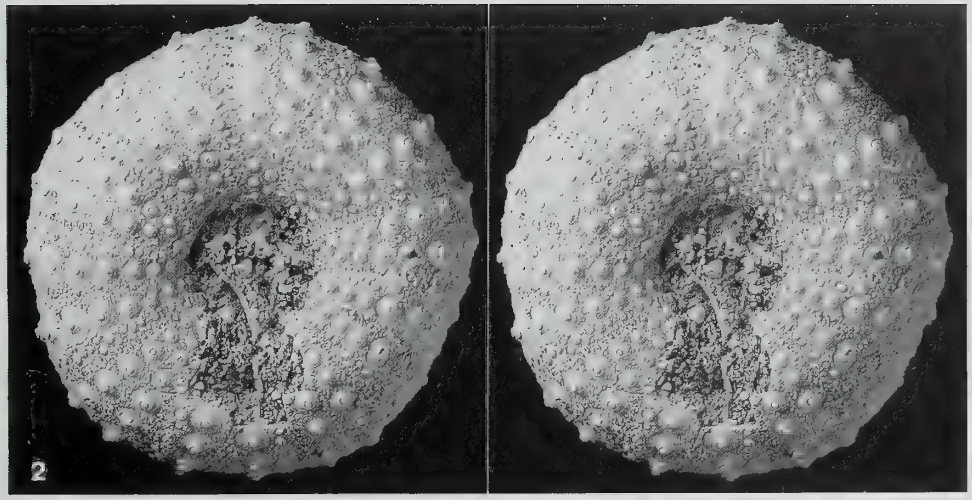
APICAL SYSTEM. No specimen retains any of the plates of the apical disc. In outline, the apical disc is pentagonal and weakly but unmistakably elongated posteriorly. There is a shallow, U-shaped notch at each interradius, of which the posterior is the largest and deepest. In length, the apical disc is 39–49% of the test diameter (mean = 43%; SD = 2·6; N = 25), while the apical disc width is 79–98% of the length (mean = 87%; SD = 5·9; N = 19). The apical disc is very slightly depressed in some individuals.

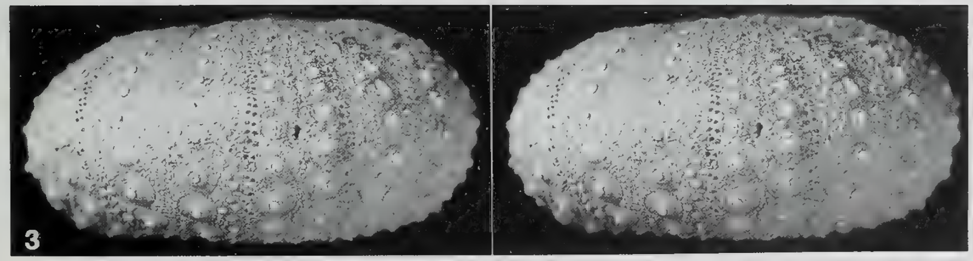
AMBULACRA. These are relatively broad and, at the ambitus, measure 23–26% of the test diameter (mean = 25%; SD = 0·8; N = 27). They are compound throughout in a trigeminous diadematoid style, each compound plate carrying a single perforate, crenulate tubercle, right up to the apex. Tubercles are largest ambitally and decrease in size gradually both adapically and adorally. Ambulacral pores are arranged in a uniserial row from apex to peristome. They are

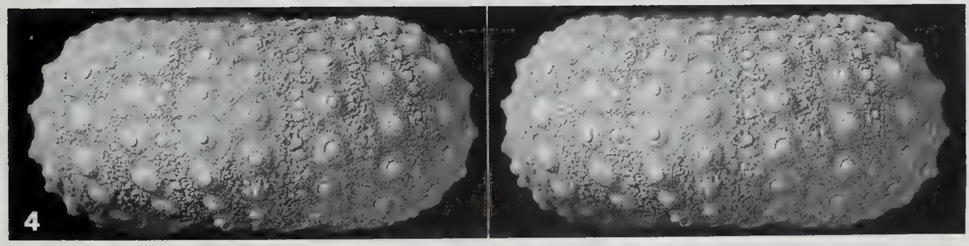
---

Plate 7
Tiaromma michelini (Agassiz)
Fig. 1 E.80084, apical. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 3·3).
Figs 2–3 E.80288: 2, oral; 3, lateral. As last (× 2).
Fig. 4 BGS GSM 118308, lateral. Upper Greensand, Warminster, Wiltshire (× 3).


1


2


3


4

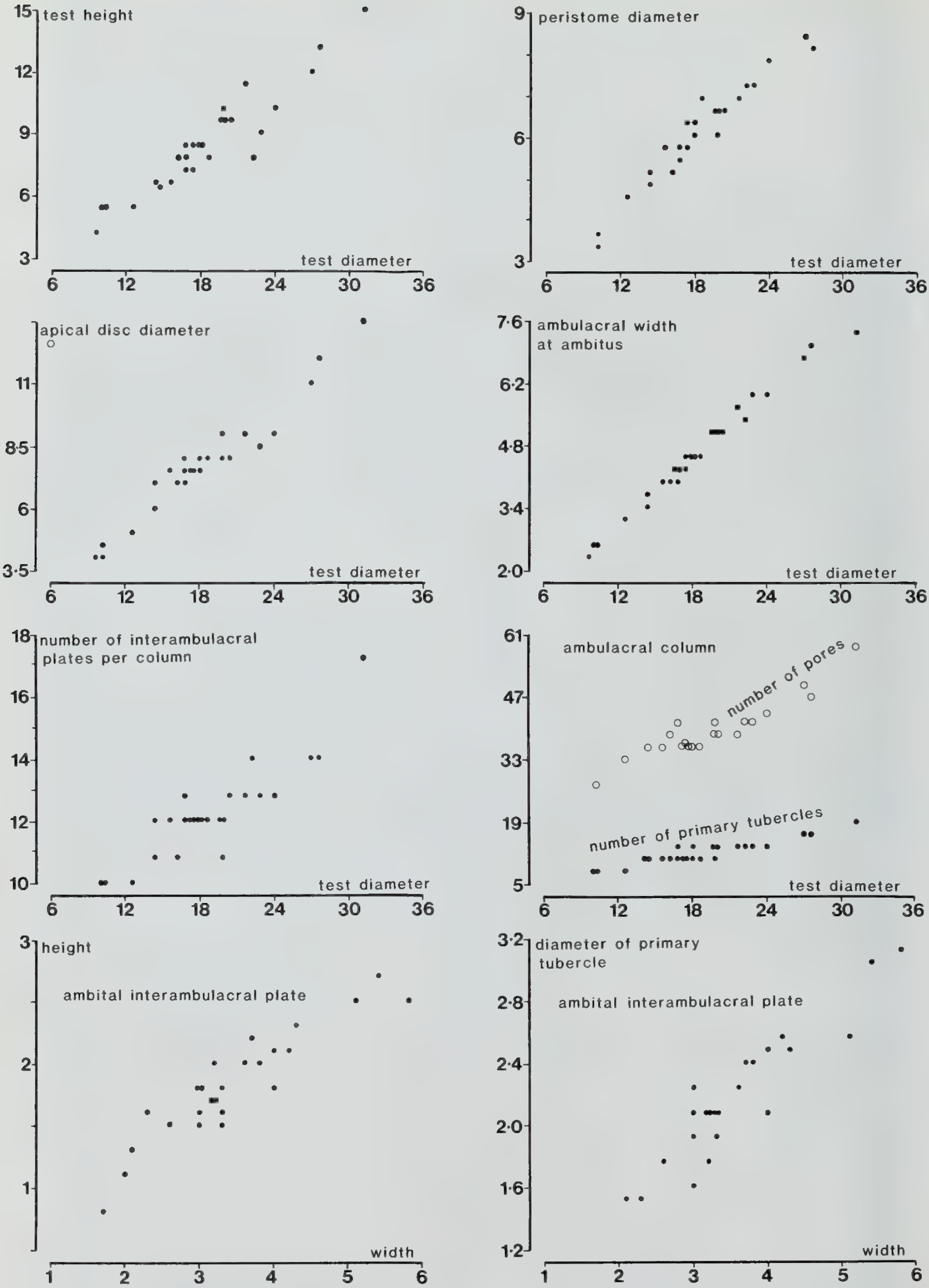


Fig. 20 Biometric data on *Tiaromma michelini* from the Lower Cenomanian of Wilmington.

P_2-type partitioned isopores and, at the ambitus, the pore zone is only 15–20% of the plate width. From just above the ambitus to the peristome the ambulacral pores are small and widely spaced; there is no adoral concentration. Miliary tubercles are inserted between succeeding ambulacral pores. Adapically, ambulacral pores become noticeably denser, the interspersed miliary tubercles disappear and succeeding ambulacral pores abut. Compound plates from just above the ambitus to the peristome are strictly trigeminous but adapically many of the compound plates comprise four elements. Ambulacral tubercles are confluent, without intervening miliary tubercles. Two miliary tubercles, one adapical the other adoral, lie on the adradial side of the primary tubercle and a row of four or five miliary tubercles lie perradially on each plate. There is therefore a zigzag biserial row of miliary tubercles running perradially down each ambulacrum. The miliary zone decreases both adorally and adapically as the ambulacrum narrows. There are 26 pores and 8 primary tubercles in an ambulacrum column at 10·3 mm test diameter, increasing to 59 pores and 18 tubercles at 31·1 mm test diameter (Fig. 20).

INTERAMBULACRA. The interambulacra are only a little broader than the ambulacra and measure 32–38% of the test diameter (approximately 1·35 times the ambulacral width) at the ambitus (mean = 35%; SD = 1·50, N = 27). There are 10 interambulacral plates per column at 10·3 mm test diameter, rising to 16 at 31 mm test diameter. Each plate has a single, moderate-sized crenulate and perforate primary tubercle. At the ambitus interambulacral plates are rather elongate with a height 43–69% of the width (mean = 53%; SD = 6·4; N = 25). The primary tubercle has a distinct areole which is oval in outline and occupies the full height of the plate and 51–73% of the plate width (mean = 62%; SD = 6·2; N = 23). All the primary interambulacral tubercles are confluent and, although miliary tubercles become sparse adapically, they are well developed in the ambital region and adorally. One or two small secondary tubercles lie near the adradial suture on ambital and subambital plates but they never approach the primary tubercles in size. These secondary tubercles lie in a distinct adradial band of miliary tubercles (Pl. 7, fig. 3). At the interradius there is a broad zone of miliary tubercles, four to six abreast in the larger specimens but only two abreast in juveniles. Adapically the primary tubercles shift progressively from their central position on each plate to lie close to the adradial suture. Furthermore, the miliary tubercles become sparse and the interradial zone becomes totally bare of tubercles about four plates below the apical disc. The most adapical plates in each column often do not reach the perradius because of the interradial notch formed by the apical disc. The naked interambulacral zone becomes very slightly depressed relative to the rest of the test in the largest specimens, but is flush in small to medium-sized individuals. Interambulacral plates are the same height as ambulacral plates and are positioned opposite one another, not alternately. At the ambitus, three ambulacral pores lie adjacent to each interambulacral plate. Interambulacral and ambulacral tubercles are much the same size throughout.

PERISTOME. The peristome is small and sunken, measuring only 26–37% of the test diameter (mean = 33%; SD = 2·5; N = 25). It is proportionally smaller in larger individuals. At 10 mm test diameter the peristome is 34% of the test diameter, but at 31 mm it is 26% of the test diameter. The oral surface of the corona is strongly curved so that the peristome opening is well above the lower part of the test. The peristome is circular and has feeble gill slits.

REMARKS. The taxonomic history of this species is rather complex, largely owing to a misidentification of Goldfuss' species *Cidarites ornatus*. This species was figured and described by Goldfuss (1829: 123; Pl. 40, fig. 10) and was said to come from the Cenomanian of Essen, Westphalia, although this age and locality were seriously questioned by Schlüter (1883: 40). Although Goldfuss quite clearly states, and shows clearly in his figure, that ambulacral pores become biserial both adorally and adapically in his species, Cotteau (1864) and later Wright (1867) figured and described a quite different species under this name, as first pointed out by Schlüter (1883). Cotteau's and Wright's species has uniserial ambulacral pores throughout.

Diadema michelini was first reported from the Cenomanian of Villers-sur-Mer by Agassiz (1840*b*) but not illustrated until 1864, when Cotteau published a description of the holotype. In the meantime, Woodward (*in* Morris, 1843) had identified specimens from the Lower Cenomanian greensand of Warminster as *Diadema ornatum* [*non* Goldfuss]. These were later described as a new species, '*Diadema benettiae* Forbes', by Woodward (1856). Specimens originally identified by Forbes as *D. benettiae* and forming the type series are in the Geological Survey Museum (BGS GSM40308–17). The best preserved of these (BGS GSM40308) is here designated lectotype of *benettiae*. Cotteau (1864: 476) correctly pointed out that *Diadema michelini* Agassiz and *Diadema benettiae* Forbes were synonymous and united the two species.

Wright (1867) complicated matters by describing and illustrating a specimen of *Polydiadema bonei* (Forbes) under the name *Pseudodiadema michelini*, (see p. 68), a misidentification which led him to maintain *Pseudodiadema michelini* and *Pseudodiadema benettiae* (Forbes) were discrete species. Having studied a plaster cast of Agassiz' type specimen of *Diadema michelini*, Forbes' type series of *D. benettiae* and the specimens illustrated by Wright under the names *Pseudodiadema michelini* and *P. benettiae*, I am convinced that *D. benettiae* Forbes and *D. michelini* Agassiz are synonymous and that the former name is therefore a junior synonym.

Cotteau (1864), Wright (1867) and most later workers believed that *Diadema michelini* Agassiz was distinct from the species which they wrongly identified as *Pseudodiadema ornatum*. Wright's (1867) *Pseudodiadema michelini* [*non* Agassiz] is, as has been said, actually *Polydiadema bonei* (Forbes) and is quite different from his *Pseudodiadema ornatum* [*non* Goldfuss]. As distinguishing features Cotteau (1864) and Wright (1867) point out that their *P. ornatum* [sic] is taller and has a narrower base, has a more deeply sunken peristome, weakly undulose lines of ambulacral pores, better developed secondary tubercles and a more elongate apical disc compared with *P. michelini*. However, close study of the Cenomanian Grey Chalk specimens that Wright (1867) ascribed to *P. ornatum* (E.40110, E.1942 and E.1554), together with other material from the same horizon, shows no significant and consistent differences on which to separate the two populations at species level. The only real differences seem to be that, on average, the population from the Grey Chalk is taller than the Wilmington one, and that, in most of the larger specimens from the Grey Chalk, the apical disc is slightly sunken, whereas specimens from the Wilmington population almost never show this. At most, the Grey Chalk population should be distinguished at subspecies level.

De Loriol (1887) proposed the name *Pseudodiadema schluteri* for the species wrongly named by Cotteau (1864) and Wright (1867) as *Pseudodiadema ornatum*, taking as the type a specimen from the Cenomanian of Portugal. This, however, has secondary interambulacral tubercles at the ambitus which are almost as large as the primary tubercles and is undoubtedly not synonymous with the *Pseudodiadema ornatum* of Cotteau and Wright.

Genus ***POLYDIADEMA*** Lambert, 1888

Polydiadema bonei (Woodward 1856)

Pl. 8, figs 1–4; Pl. 40, figs 2, 3; Figs 21, 22.

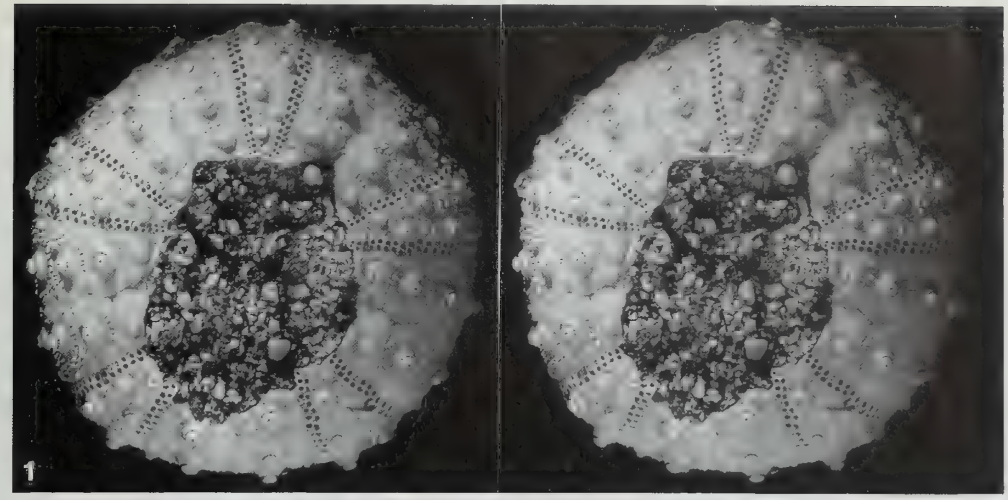
1854 *Diadema Bonei* Forbes, *in* Morris: 76 [*nomen nudum*].
1856 *Diadema Bonei* Forbes; Woodward: 8.
1864 *Pseudodiadema tenue* Desor; Cotteau: 471 (*partim*).
1864 *Pseudodiadema pseudo-ornatum* Cotteau: 486; pl. 1116, figs 5–15.
1867 *Pseudodiadema Michelini* Wright (*non* Agassiz): 99; pl. 19, fig. 2.
1910 *Polydiadema Boneti* [sic] (Forbes) Lambert & Thiéry: 190.
1910 *Pseudodiadema pseudoornatum* (Cotteau) Lambert & Thiéry: 190.
1963 *Polydiadema pseudo-ornatum* (Cotteau); Cayeux: 19; fig. 8.

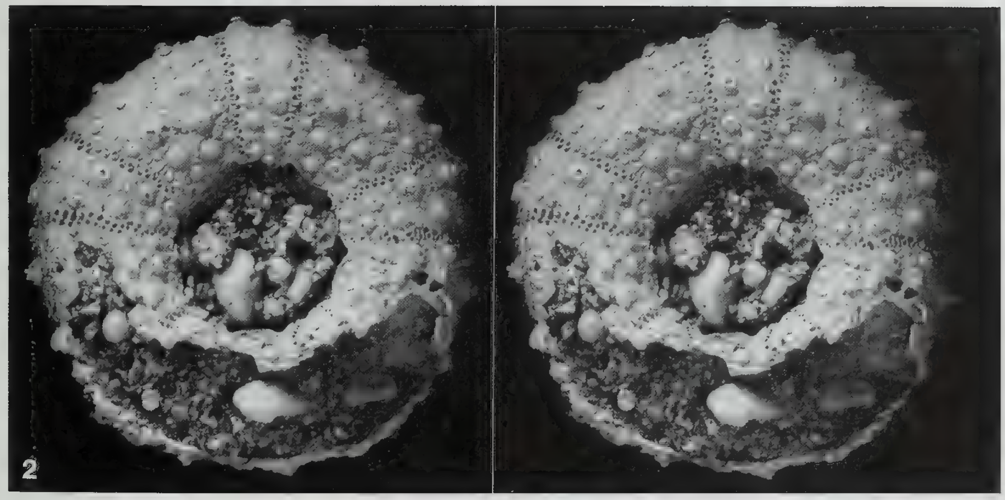
Plate 8

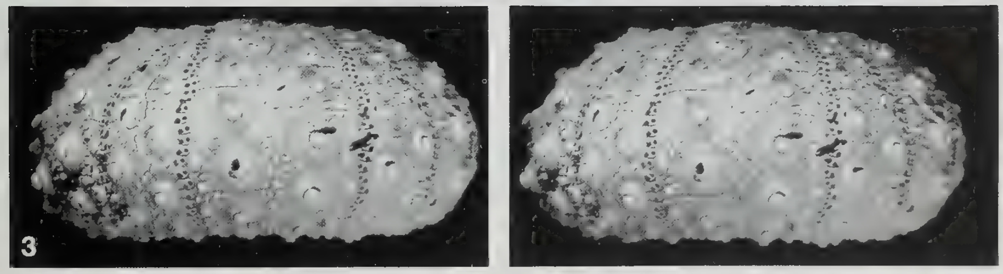
Polydiadema bonei (Woodward)

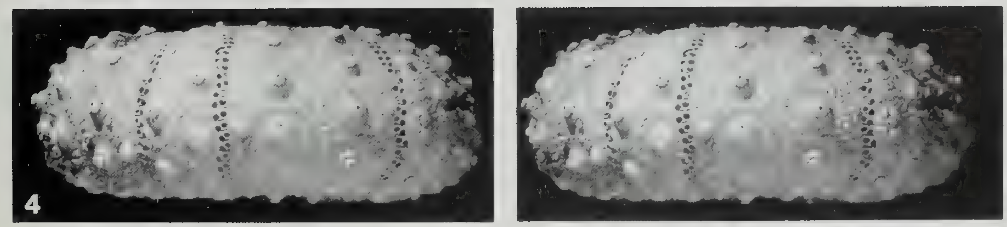
Figs 1, 2, 4 E.81227: 1, apical; 2, oral; 4, lateral. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 3·5).

Fig. 3 E.81204 (tall variety), lateral. As last (× 4).


1


2


3


4

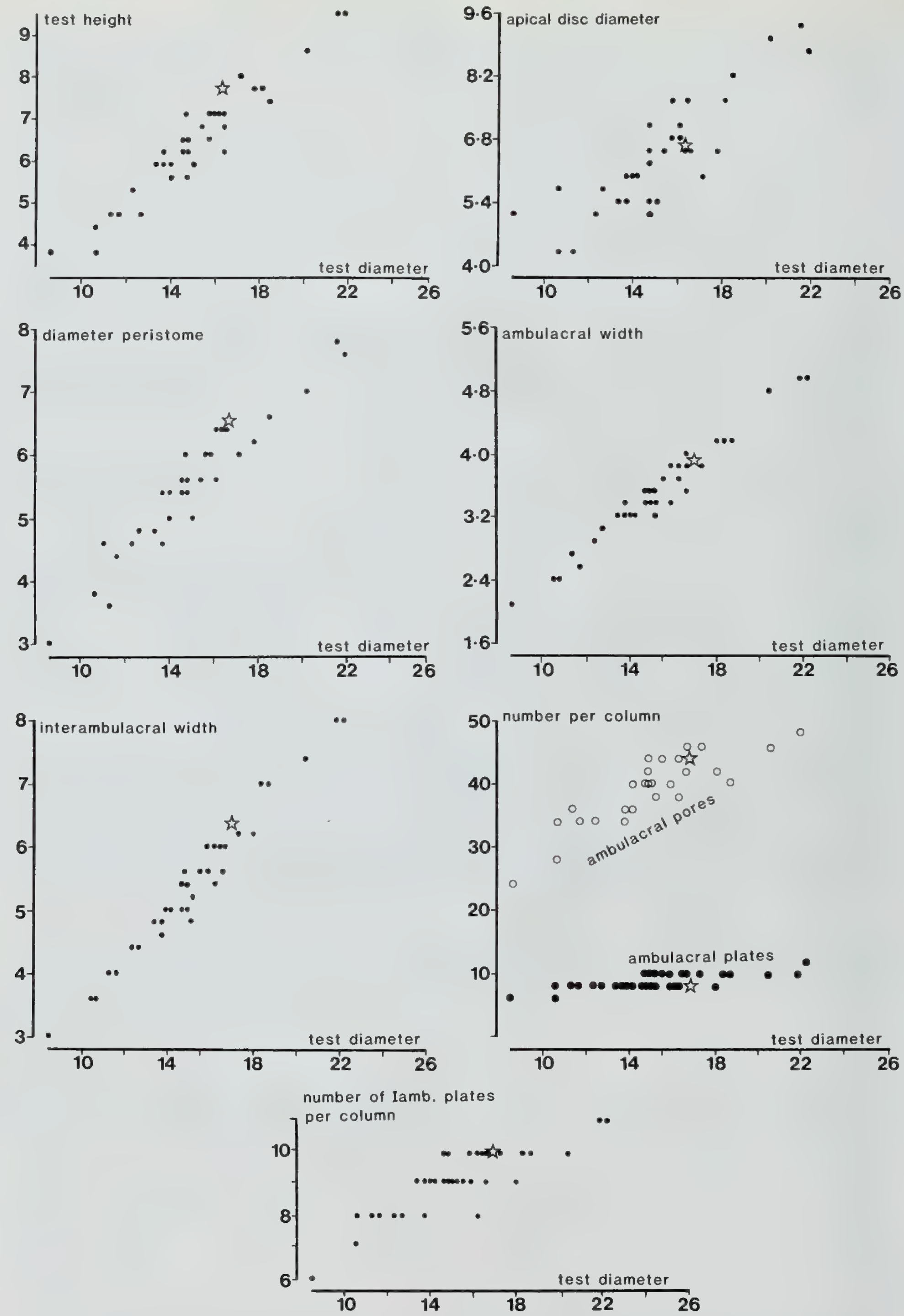


Fig. 21 Biometric data on *Polydiadema bonei* from the Lower Cenomanian of Wilmington. ☆ = lectotype from Warminster.

Amended diagnosis. A species of *Polydiadema* with a flattened, wheel-shaped test, with 8 to 11 interambulacral plates per column at 10 to 22 mm test diameter, each with a single primary tubercle occupying one third of the plate width. Subambital plates have in addition a smaller secondary tubercle adradially. Compound ambulacral plates are composed of five elements ambitally but only four adorally. An adapical naked zone is present. The peristome is sunken and about 37% of the test in diameter; the apical disc is only slightly larger.

Lectotype. British Geological Survey no. GSM48326, here selected. See pp. 68–69.

Material. Eighty-three specimens of this species were collected in the White Hart Pit, Wilmington, of which 34 of the best preserved were used in a biometrical study (E.77681, E.76291–4, E.81199–227). Of these 83 specimens, 52 were accurately located within the stratigraphical succession. In addition, many specimens from the Lower Cenomanian greensand of the Warminster district were also examined.

Stratigraphical occurrence and distribution. At Wilmington, *P. bonei* is found in the Grizzle and the Wilmington Sand, from 124 cm to 621 cm below the standard datum level. They therefore come from the Lower Cenomanian. This species is most abundant between 200 cm and 300 cm below standard datum (the lower part of the Grizzle), where more than half of the specimens were collected (Fig. 7, pp. 18–19). Below about 400 cm, specimens are rare. Elsewhere in Britain, this species is fairly common in the Lower Cenomanian greensands of Warminster and Dorset.

Description. *SHAPE AND SIZE.* Tests range in size from 8·6 to 22·3 mm in diameter (mean = 15·2 mm; SD = 3·0; N = 34). They are either perfectly circular or very slightly pentagonal in outline with the ambulacra at the corners of the pentagon. The test is relatively flat and test height is 35–48% of the diameter (mean = 42%; SD = 2·7; N = 34). The oral surface is rather convex, so that the peristome is moderately sunken. The apical surface is weakly convex or more or less flat. Some forms are wheel-shaped and in profile the sides are uniformly curved and the ambitus is at mid-height. Others, however, are slightly conical in profile and the ambitus lies a little below mid-height. Ambulacral and interambulacral tubercles are equally developed and prominent, giving the test a strongly tuberculate appearance.

APICAL DISC. No specimen has any of the apical disc plates preserved in position and they must have dissociated rapidly upon death. In outline, the apical disc is pentagonal and there are small, U-shaped notches at the interradial sutures. The apical disc is 35–48% of the test diameter (mean = 42%; SD = 2·7; N = 31) and is always the highest point on the test.

AMBULACRA. These are moderately broad and measure 21–24% of the test diameter (mean = 23%; SD = 0·8; N = 34). Except for the most adapical plates, ambulacral plates are compound in a polygeminous diadematoid style (Fig. 22). At the ambitus and adapically there are five elements in each compound plate but in the three or so plates closest to the peristome

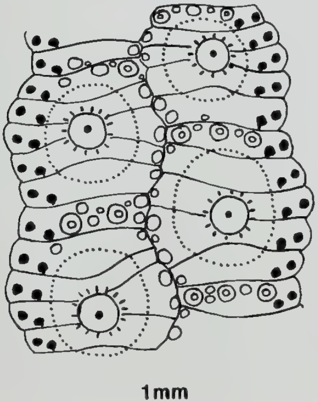


Fig. 22 Camera lucida drawing of ambital ambulacral plate arrangement in *Polydiadema bonei* (E.81204) from the Lower Cenomanian of Wilmington.

in each column there are only four elements in each. There is a single large tubercle on each compound plate. These primary tubercles are perforate and crenulate and are largest ambitally, reducing in size gradually both adapically and adorally. In the most adapical plates, the primary ambulacral tubercles are too small to cover all five plates and overlie just two or three of the plates leaving the others unbound. There are five compound ambulacral plates and 24 ambulacral pores per column at 8·6 mm test diameter, increasing to 10 or 11 compound plates and about 50 ambulacral pores at 22·3 mm test diameter. Ambulacral pores are P_1 and P_2 type partitioned isopores. They are arranged in a straight line adapically and adorally but are very slightly sinuous at the ambitus. There is no noticeable concentration of ambulacral pores towards the peristome. At the ambitus, ambulacral plates are squarish in shape and the pore zone forms about 25% of the width of the plate. Ambulacral tubercles are non-confluent. There is a uniserial row of miliary tubercles along the perradius. Where horizontal and vertical rows of miliaries meet there is a small cluster of three or four miliary tubercles.

INTERAMBULACRA. Interambulacral zones are about 1½ times as broad as ambulacral zones and, at the ambitus, their breadth is 31–38% of the test diameter (mean = 35%; SD = 1·4; N = 34). They are slightly broader proportionally in larger individuals. There are six interambulacral plates per column at 8·6 mm test diameter, rising to 11 by about 22 mm test diameter (Fig. 21). At the ambitus, individual plates are broader than tall and plate height is 56–69% of plate width (mean = 63%; SD = 3·9; N = 33). Each plate carries a single large tubercle, positioned centrally; it is perforate and crenulate and occupies about one third of the plate width at the ambitus. The mamelon is relatively small in relation to the size of the tubercle. Subambitally, a smaller secondary tubercle appears near the adradial margin of the plate, but this is lost towards the peristome. The primary tubercles are confluent adorally, but from the ambitus adapically a single row of miliary tubercles separates succeeding tubercles. To the adradial side of each primary tubercle there is an irregular array of variously-sized miliary tubercles, some two abreast. There is also a broad zigzag row of miliaries, up to four abreast (two on each plate) at the interradius. This narrows to just two miliaries abreast both adapically and adorally. Above the ambitus, miliary tubercles become much sparser, so much so that the most adapical two or three interambulacral plates in each column have a naked interradial zone. The adapical horizontal row of miliary tubercles also becomes progressively more sparse adapically. The naked interradial zone is generally not noticeably depressed. At the apex of the interambulacrum there is a shallow, U-shaped notch interradially which may separate the most adapical interambulacral plate in each column from its neighbour in the adjacent column. Although the primary tubercles are roughly uniform in size from the subambital region to about half-way up the apical surface, the most adapical two tubercles in each column are much reduced in size.

PERISTOME. The peristome is circular in outline with a diameter 32–43% of the test diameter (mean = 37%; SD = 2·4; N = 31). It is slightly smaller than the apical disc. As the apical surface is strongly convex, and the most adoral plates curve inwards, the peristome is moderately sunken. Buccal slits are broad and relatively shallow.

REMARKS. The taxonomic history of this species is complex and confused. Its earliest mention appears in Morris (1854), where the name *Diadema bonei* Forbes is given without description or illustration. Two years later Woodward (1856) published an adequate diagnosis, thus establishing the validity of the species. Woodward also described a second species, *Diadema benettiae* Forbes (see p. 64), from the same locality and horizon as *D. bonei* (Upper Greensand of Warminster), and suggested that *D. bonei* might be synonymous with *D. michelini* Agassiz. No type for *D. bonei* was specified, although Woodward's description is obviously based upon a single specimen. The collections of the British Geological Survey contain the specimens which Forbes identified as *D. bonei* in Huxley & Etheridge (1865). These specimens, numbered BGS GSM48324–34, presumably include the one that was described by Woodward. Of the eleven specimens, GSM48325 is missing, GSM48327 is a juvenile *Tetragramma variolare* (Brongniart), GSM48330 is a juvenile *Tiaromma michelini* (Agassiz) and GSM48331–4 are *Glyptocyphus difficilis* (Agassiz). Thus only four, including the two largest, correspond to Woodward's description of *Diadema bonei* Forbes. The actual specimen described by Woodward (*op. cit.*) is stated to be '9 lines in diameter' ($=\frac{3}{4}$ of an inch or 18 mm approximately) and 4 lines in height ($=\frac{1}{3}$ of an inch or approximately 8 mm). The best-preserved of the four remaining specimens (GSM43826) measures 17 mm in diameter and 8 mm in height and is almost certainly that studied by Woodward. I therefore select BGS GSM43826 as the lectotype of *Diadema bonei* Forbes; Woodward, 1856.

Wright (1868) restudied all of Forbes' material and concluded that *Diadema bonei* Forbes was synonymous with *Diadema michelini* (Agassiz) and distinct from *Diadema benettiae* Forbes. Wright based his identification of *D. michelini* not on Agassiz' holotype but on a specimen sent to him by M. Michelin which was collected from Villers-sur-Mer. Unfortunately this specimen was apparently not conspecific with *D. michelini* Agassiz since Wright, after studying it, had no hesitation in synonymizing *D. bonei* Forbes and *D. michelini*. Therefore the description and illustration of *Pseudodiadema michelini* Wright [*non* Agassiz] in Wright (1867: 99; pl. 19, fig. 2) refers to *Polydiadema bonei* (Forbes) and described a form totally distinct from *Tiaromma michelini* (Agassiz).

To add to the confusion, Wright (1868) also described and illustrated the species *Diadema benettiae* Forbes on the basis of two BM(NH) specimens E.1610 and E.12548. This is in complete agreement with Forbes' original concept of the species, but, because Wright mistakenly identified *Polydiadema bonei* (Forbes) as *Pseudodiadema michelini*, he believed that *D. benettiae* Forbes and *D. michelini* should be retained as valid species. In actual fact, *D. benettiae* Forbes and *D. michelini* Agassiz are synonymous (see p. 64) and the specimens illustrated by Wright (1868) as '*Pseudodiadema michelini*' are *Polydiadema bonei* (Forbes). The specimens given as '*Pseudodiadema benettiae*' are in reality *Tiaromma michelini* (Agassiz).

Cotteau (1864) also described and figured a specimen under the name *Pseudodiadema pseudoornatum*. I have not examined this specimen personally, but judged from the figures and description it may well prove to be a junior synonym of *Polydiadema bonei* (Forbes).

Cotteau (1864) considered *Diadema bonei* Forbes to be a junior synonym of *D. tenue* Agassiz, although he pointed out a number of minor differences. Plaster casts in the BM(NH) of the specimens in Neuchâtel Museum (X54) originally referred to this species by Agassiz (1840*a*) show significant differences which suggest that the two species should be maintained. *Polydiadema tenue* (Agassiz) has a much larger apical disc and the interambulacral plates at the ambitus are much taller and more squarish than plates in similar-sized specimens of *P. bonei*. However, confirmation that these species are distinct must await a detailed restudy of a suitable population of *P. tenue*.

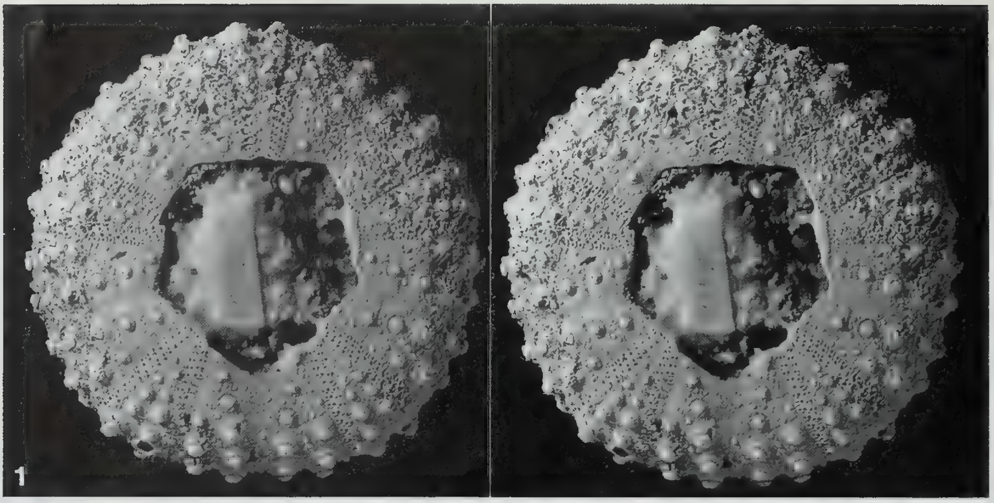
Genus ***TETRAGRAMMA*** Agassiz, 1840*a*

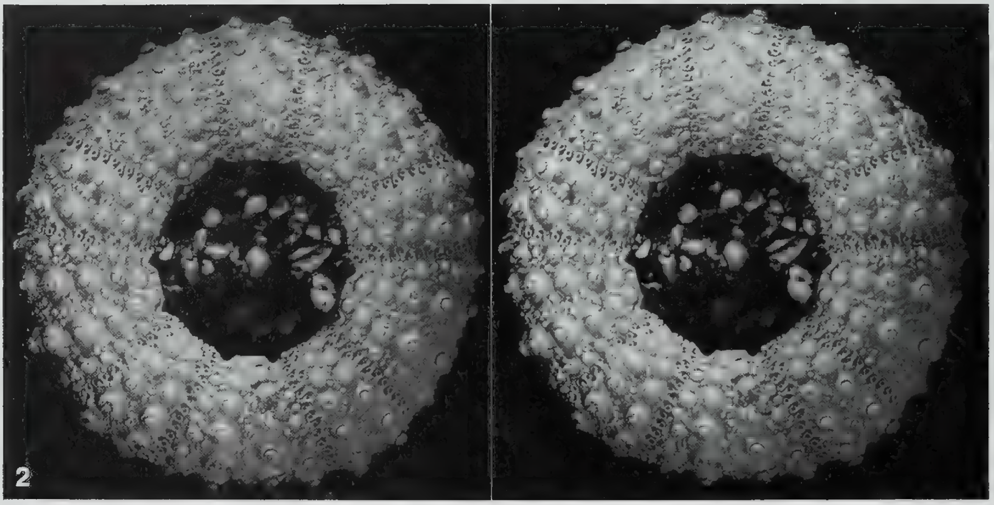
Tetragramma variolare subnudum (Agassiz 1846)

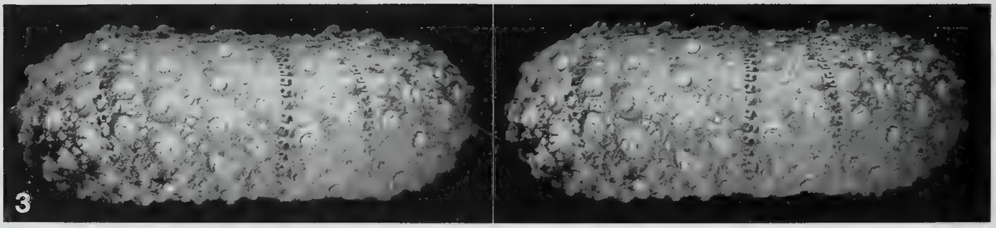
Pl. 9, figs 1–4; Fig. 23.

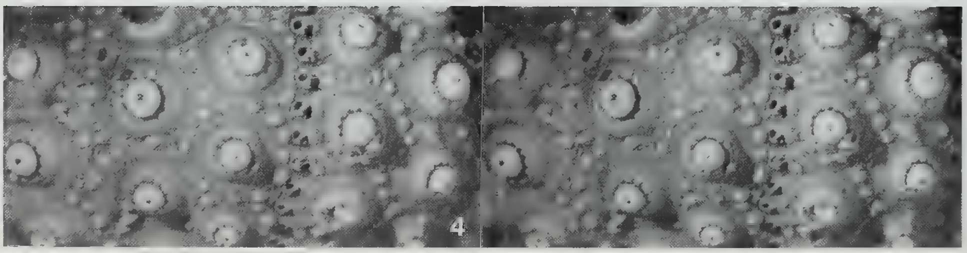
1822 *Cidarites variolaris* Brongniart: 84, 390 [*partim*]; pl. 5, fig. 9.
1846 *Diadema* (*Tetragramma*) *sub-nudum* Agassiz, *in* Agassiz & Desor: 350.
1850 *Tetragramma sub-nudum* (Agassiz) Sorignet: 26.
1854 *Diadema sub-nudum* Agassiz; Morris: 77.
1856 *Diadema sub-nudum* Agassiz; Woodward: 10.
1858 *Diplopodia subnuda* (Agassiz) Desor: 78.
1864 *Pseudodiadema variolare* (Brongniart) var. *sub-nuda* (Agassiz) Cotteau: 488; pl. 1118, figs 1–12.
1867 *Pseudodiadema variolare* (Brongniart) Wright: 107 [*partim*]; pl. 18, fig. 2.
1874 *Pseudodiadema variolare* (Brongniart); Quenstedt: 321 [*partim*]; pl. 72, fig. 70.
1883 *Pseudodiadema variolare* (Brongniart); Schlüter: 38 [*partim*].
1894 *Diplopodia variolaris* (Brongniart) Lambert: 52 [partim] (see also for full synonymy).
1963 *Tetragramma variolare* (Brongniart) var. *sub-nuda* Cayeux: 21.

DIAGNOSIS. A subspecies of *Tetragramma variolare* in which the apical surface is very slightly sunken and the most adapical two or three compound ambulacral plates in each column lack primary tubercles. Adapically, the pore zones form almost the entire width of the ambulacral zone and the interambulacral tubercles decrease sharply in size.


1


2


3


4

MATERIAL. Twenty-nine individuals from the pit at Wilmington (E.80113–41) were used in the biometrical study. Thirteen of these were located accurately within the stratigraphical succession. A further 42 specimens (E.80142–83) have accurate stratigraphical localization and a large number of other specimens were collected loose. Populations of *T. variolare* from the Cenomanian of Chard, Warminster and Folkestone were examined for comparison.

STRATIGRAPHICAL OCCURRENCE AND DISTRIBUTION. At Wilmington, the species occurs most commonly in the upper part of the Wilmington Sands between 400 cm and 600 cm below standard datum (Fig. 7, pp. 18–19). It is also present, though not common, in the Grizzle and one specimen was collected from the Cenomanian Limestone at 53 cm below standard datum. The total range of this species at Wilmington is therefore from 53 cm to 690 cm below standard datum (Fig. 7); thus it is found in the Lower and Middle Cenomanian. Elsewhere in Britain the species is found in the Lower Cenomanian greensands of Warminster, the Middle Cenomanian Chloritic Marl of Chard, Somerset and the Grey Chalk of the Dover region. Those from the Chloritic Marl of Chard and the greensands of Warminster belong to the same subspecies as the Wilmington population, but those from the Grey Chalk of Dover correspond to *T. variolare, sensu stricto.*

DESCRIPTION. *SHAPE AND SIZE.* Tests range in size from 8·5 to 25·7 mm in diameter (mean = 17·2 mm; SD = 4·6; N = 29). They are circular to weakly pentagonal in outline and flattened in profile. Test height is 34–44% of the diameter (mean = 39%; SD = 2·5; N = 29), which is significantly less than in any other pseudodiadematid from Wilmington. In profile, the sides are uniformly curved and the ambitus is at approximately mid-height or sometimes very slightly higher. Oral and adapical surfaces are very broad and flat in profile and characteristically the adapical surface is slightly broader than the oral surface (Pl. 9, fig. 3). Ambulacral and interambulacral tubercles are of equal size at the ambitus and adorally; adoral tuberculation is noticeably coarser and denser than adapical tuberculation.

APICAL SYSTEM. The plating of the apical system is unknown. It is more or less flush with the upper surface or very slightly sunken, the corona being flat or very slightly sunken adapically. In outline, the apical system is pentagonal with the angles of the pentagon at each interradius, which is weakly notched. In larger specimens, the apical disc may be slightly longer than broad but in small to medium-sized individuals the outline of the apical disc is more or less equidimensional.

AMBULACRA. Ambulacral zones are relatively narrow and, at the ambitus, measure 15–23% of the test diameter (mean = 21%; SD = 2·2; N = 29). From the peristome to a little above the ambitus ambulacral plates are compound in the diadematoid style and are strictly trigeminous. Each carries a single, large primary tubercle. At the ambitus, ambulacral plates are slightly wider than tall (plate height is on average 83% of plate width) and the pore zone forms 20–25% of the plate width. Adapically, primary tubercles diminish rapidly in size and there are four elements to each compound plate. Towards the top, primary tubercles disappear altogether, ambulacral plates return to being simple and the perradial zone, which adambitally has the tubercles, wedges out to almost nothing. At the apex, the entire width of the ambulacra is formed by the pore zones (Pl. 9, fig. 1). Ambulacral pores are partitioned isopores, type P_3 adorally and type P_2 ambitally and adapically. At the ambitus, ambulacral pores are arranged uniserially in a straight line, but they become more crowded and offset in triads close to the peristome, forming phyllodes. There are 6 to 12 pores in each phyllode dependent upon size. A little above the ambitus the ambulacral pores become biserially arranged in each column (Pl. 9, figs 3, 4).

Plate 9

Tetragramma variolare subnudum (Agassiz)

Fig. 1 E.80122, apical. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 4).

Figs 2, 3 E.80121: 2, oral; 3, lateral. As last (× 4·5).

Fig. 4 E.80132, detail of ambital plating (ambulacral plates can be seen to right, interambulacral plates to left). As last (× 8).

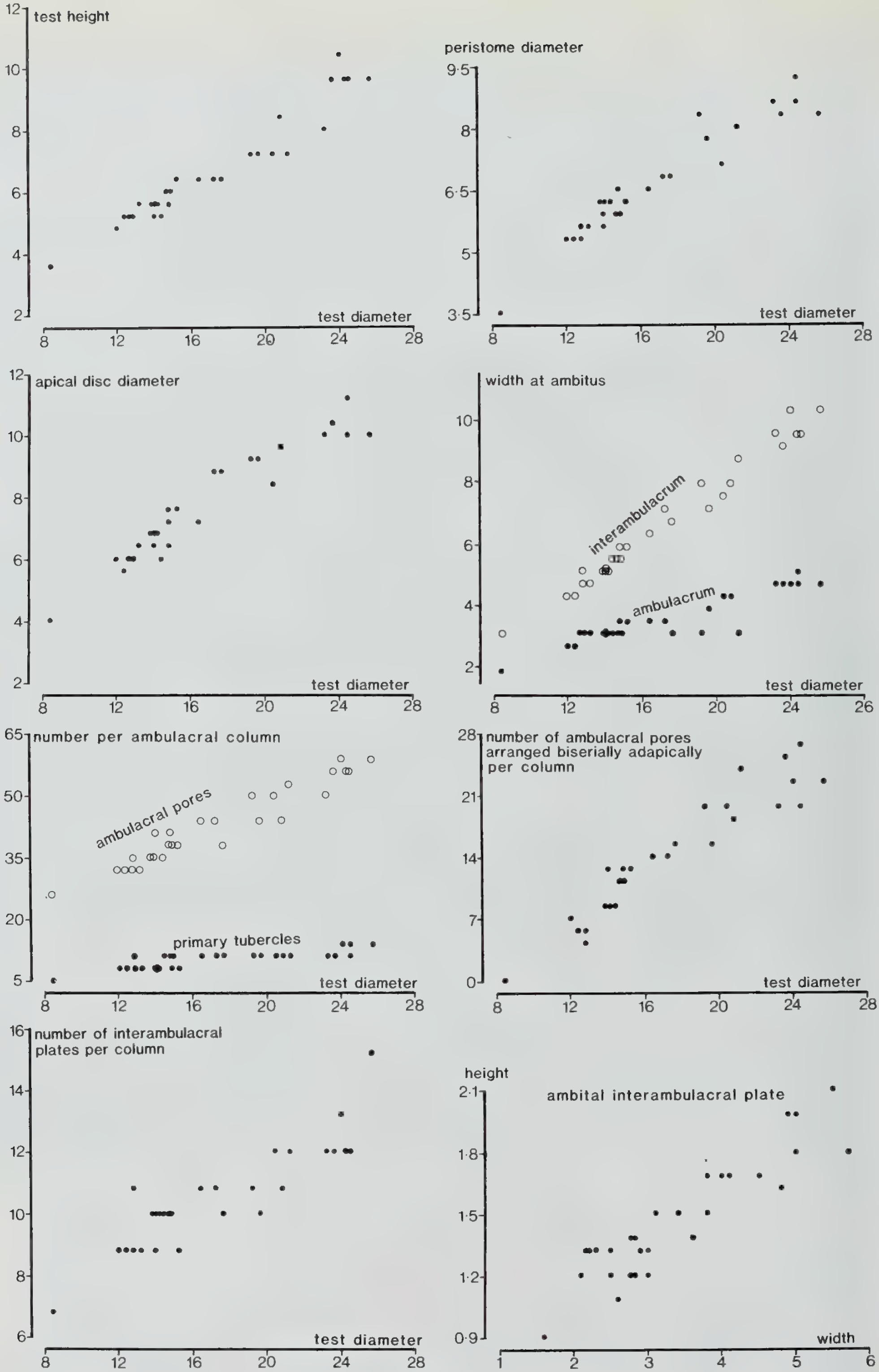


Fig. 23 Biometric data on *Tetragramma variolare subnudum* from the Lower Cenomanian of Wilmington.

There are 25 ambulacral pores and 6 primary tubercles in each ambulacral column at 8·5 mm test diameter, rising to 58 ambulacral pores and 14 primary tubercles at 25·7 mm test diameter (Fig. 23). At 8·5 mm test diameter the ambulacral pores are arranged uniserially to the very apex, but by 12 mm test diameter the six most adapical pores in each column are arranged biserially and by 20–25 mm test diameter the zone of biserial ambulacral pores contains 23 to 25 isopores. Primary tubercles are confluent and, although miliary tubercles are present, they are sparsely distributed. There is a miliary tubercle at each corner of the ambulacral plates and a single zigzag row of miliary tubercles perradially which separates the two columns of tubercles.

INTERAMBULACRA. Interambulacral zones are relatively broad, measuring 34–42% of the test diameter at the ambitus (mean = 38%; SD = 2·0; N = 29). Ambulacral and interambulacral tubercles are equal in size at the ambitus and three ambulacral pores lie against each interambulacral plate. At 8·5 mm test diameter there is only a single primary tubercle per plate. By 13·5 mm test diameter there is a second slightly smaller tubercle on ambital and adoral plates situated adradially to the primary tubercle. In larger specimens these two tubercles have become more or less the same size and appear on superambital plates as well. In some of the largest specimens a third, smaller, tubercle may also be present towards the adradial edge of subambital plates. The interambulacral plates in the ambital and adoral regions are kinked and so the two principle rows of tubercles in each column appear to alternate (Pl. 9, figs 3, 4). Adapically, tubercles diminish in size rapidly and all but the primary tubercles disappear from the highest two or three plates. At 8·5 mm test diameter there are 7 interambulacral plates per column, rising to 14 plates at 25·7 mm test diameter (Fig. 23). All tubercles are perforate and crenulate. The areoles are non-confluent at the ambitus, where there is a single circle of miliary tubercles around each large tubercle. At the interradius there is a double zigzag row of miliary tubercles from the peristome to a little above the ambitus, but adapically these miliary tubercles rapidly disappear leaving a broad, tubercle-free tract. In large specimens the three or four interambulacral plates closest to the apex have relatively few miliary tubercles and these are arranged into a single horizontal line between primary tubercles. In this region the primary tubercles are situated close to the adradial edge of each plate.

PERISTOME. This is very slightly sunken and circular in outline. It is relatively small, measuring only 33–44% of the test diameter (mean = 40%; SD = 3·2; N = 27). Buccal slits are present but are relatively shallow and unobtrusive.

DISCUSSION. The species was originally described and figured by Brongniart (1822) on the basis of specimens from the Cenomanian chalk of Le Havre. It was first reported from Britain by Morris (1843) who listed it as coming from the Chalk of Lewes and Lyme and the Greensand of Wiltshire. Agassiz, *in* Agassiz and Desor (1846), recognized three closely related species, all of which he placed in his subgenus *Tetragramma*. In addition to *Tetragramma variolare*, *sensu stricto*, he recognized the species *T. Roissyi* and *T. subnudum* and this last species he diagnosed (p. 350) as follows: 'les tubercles interambulacraires disparaissent en parti près du somet. Pores dédoublés'. In the second edition of Morris' Catalogue of British Fossils (1854) both *Diadema subnudum* and *D. variolare* are recognized from Britain. Similarly Woodward (1856) also distinguished specimens from the Grey Chalk of Dover as *Diadema variolare* and specimens from the Upper Greensand of Warminster as *D. subnudum*. Cotteau (1864) recognized *subnudum* and *roissyi* only as varieties of *variolare*. He pointed out that the variety *sub-nuda* was almost bare of tubercles adapically and that amongst Brongniart's original material of *Cidarites variolare* was a specimen of this variety. Cotteau suggested that *sub-nuda* was a northern form and that it was replaced in central and southwestern France by the variety *roissyi*. Wright (1867) also believed that *subnudum* and *roissyi* were only varieties of *Tetragramma variolare*. He noted that *Tetragramma variolare*, *sensu stricto*, was found in the Upper Greensand of Warminster and the Chloritic Marl of Chard whereas the variety *subnudum* was known only from the Chloritic Marl of Chard.

T. variolare subnudum is treated as a valid subspecies largely because the entire population from Wilmington corresponds to this morphotype. It is characterized by having (i) ambulacral tubercles absent from the adapical region of the ambulacra, (ii) ambulacral pore zones forming almost the entire width of the ambulacra adapically, and (iii) a sharp and distinct reduction in the size of interambulacral tubercles adapically. Identical forms come from the Cenomanian Chloritic Marl as pointed out by Wright (1867).

Genus *ALLOMMA* Pomel, 1883

Allomma rhodani (Agassiz 1840)

Pl. 10, figs 1–4; Fig. 24

1840*b*	*Diadema Lucae* Agassiz: 8 [*nomen nudum*]. See p. 77.
1840*b*	*Diadema Rhodani* Agassiz: 8 [*nomen nudum*].
1840*a*	*Diadema Lucae* Agassiz: 8; pl. 16, figs 11–15.
1840*a*	*Diadema Rhodani* Agassiz: 9; pl. 16, figs 16–18.
1854	*Diadema Rhodani* Agassiz; Morris: 70.
1856	*Diadema Desori* Forbes; Woodward: 8.
1856	*Diadema pustulatum* Forbes; Woodward: 8.
1864	*Pseudodiadema Rhodani* Desor; Cotteau: 460; pl. 1110, figs 1–11.
1868	*Pseudodiadema Rhodani* (Agassiz); Wright: 96; pl. 18, fig. 3.
1908	*Polydiadema rhodani* (Agassiz) Valette: 64.
1955	*Polydiadema rhodani* (Agassiz); Szörényi: 171; pl. 1, figs 18–20, 27.

MATERIAL. Twelve specimens only have been collected from the quarry at Wilmington, four of which were located within the stratigraphical succession. Eight of these (E.80020–5, E.80028–30) together with four well-preserved specimens from the Lower Cenomanian greensands of Warminster (E.75746a–c, E.34241) and a large specimen from the Middle Cenomanian Chloritic Marl of Chardstock, Dorset (E.1606) formed the basis of the biometric study. Plaster casts of the types of *Diadema rhodani* Agassiz and *Diadema lucae* Agassiz were examined for comparison.

STRATIGRAPHICAL OCCURRENCE AND DISTRIBUTION. At Wilmington, *A. rhodani* is found in the Wilmington Sands between 328 cm and 605 cm below standard datum. The species is also known from the Lower Cenomanian greensands of the Warminster district, Wiltshire and in the glauconitic Basement Bed at Chardstock, Dorset. The specimens from the Basement Bed are lightly phosphatized, suggesting that they belong to the *Turrilites acutus* assemblage of the *A. rhotomagense* Zone, Middle Cenomanian.

DESCRIPTION. *SHAPE AND SIZE.* Tests range in size from 6·5 mm to 28·0 mm in diameter, although at Wilmington no specimens larger than 13·0 mm in diameter were found. Test height ranges from 3·4 to 12·3 mm, which is 44–54% of the test diameter (mean = 49%; SD = 3·5; N = 12). The test is circular in outline and in profile is slightly conical (Pl. 10, figs 3, 4). The base is broad and flat while the apical surface is smaller and set very slightly oblique to the base. The ambitus lies about $\frac{1}{3}$ of the height of the test above the base. At the ambitus ambulacral tubercles are almost as large as interambulacral ones.

APICAL DISC. Plates of the apical disc are not preserved in any of the specimens. The outline of the apical disc is pentagonal and, in diameter, measures 34–46% of the test diameter (mean = 39%; SD = 3·6; N = 11). It is proportionally larger in juveniles, measuring 46% of the test diameter at 6·5 mm but only 34% at 28·0 mm. There is a shallow but distinct V-shaped notch at each interradius forming an angle of the pentagon.

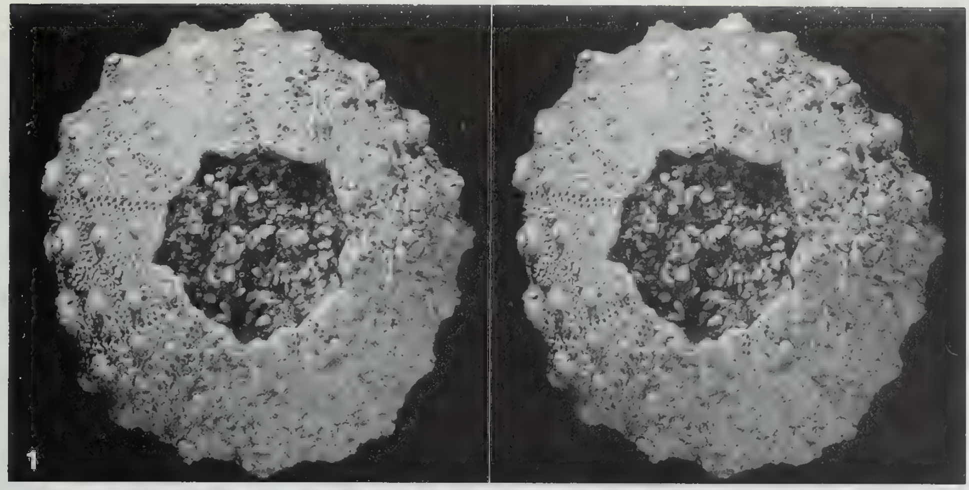
Plate 10

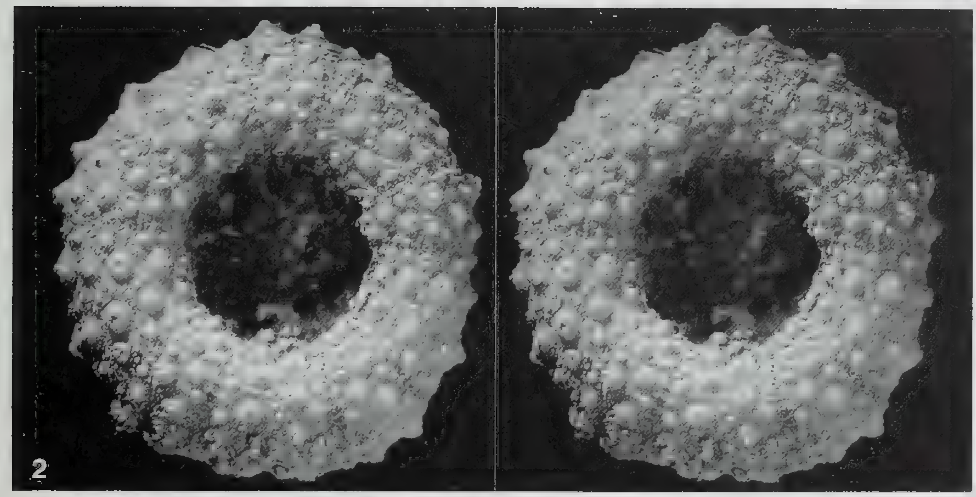
Allomma rhodani (Agassiz)

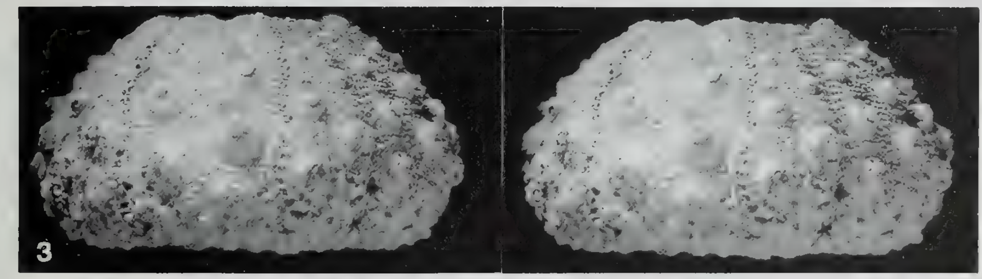
Figs 1, 3 E.80024: 1, apical; 3, lateral. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (×4·5).

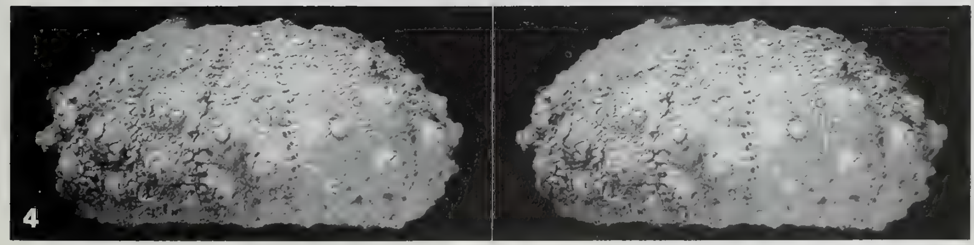
Fig. 2 E.80022, oral. As last (×8·5).

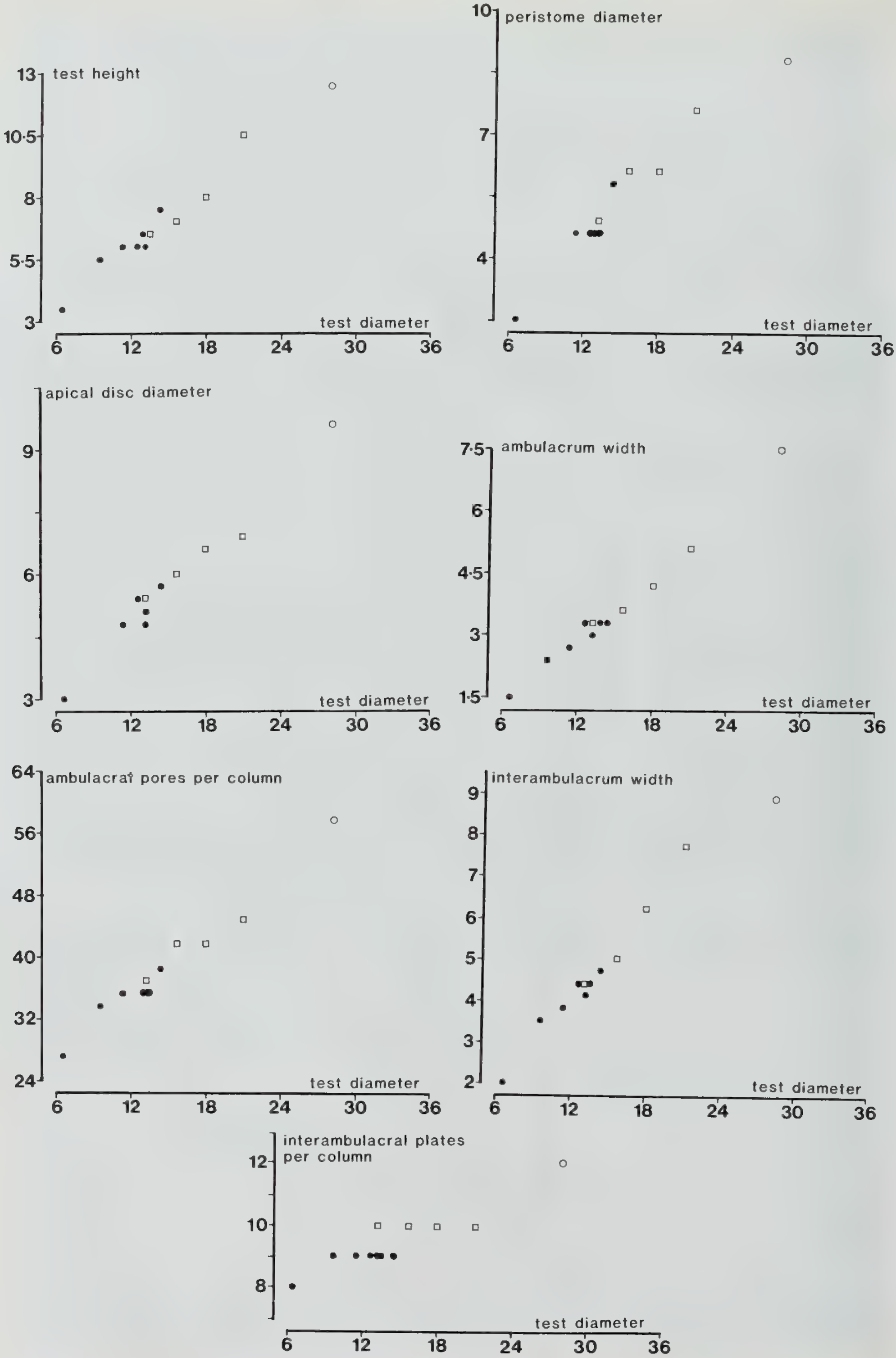
Fig. 4 E.80029, lateral. As last (×5).


1


2


3


4


test height
13
10·5
8
5·5
3
peristome diameter
10
7
4
apical disc diameter
9
6
3
ambulacrum width
7·5
6
4·5
3
1·5
ambulacral pores per column
64
56
48
40
32
24
interambulacrum width
9
8
7
6
5
4
3
2
interambulacral plates per column
12
10
8
test diameter
6
12
18
24
30
36

AMBULACRA. These are relatively broad at the ambitus, where they have a breadth of 23–26% of the test diameter (mean = 25%; SD = 1·0; N = 12), but taper markedly adapically. Ambulacral plates are compound in the polygeminous diadematoid style with five ambulacral pores to each compound plate. Ambulacral pores are P_1 or P_2-type partitioned isopores and are arranged in single lines which are straight adapically and adorally but noticeably undulose ambitally. There is not the slightest development of pore crowding towards the peristome. The pore zone forms only about 20% of the plate width at the ambitus. There are 27 ambulacral pores and 6 primary tubercles per column at 6·5 mm test diameter; this increases to 57 ambulacral pores and 11 primary tubercles at 28·0 mm test diameter. At the ambitus the primary tubercles are only very slightly smaller than the interambulacral tubercles and there is one large tubercle per compound plate. Each tubercle is surrounded by a single circle of miliary tubercles. Immediately subambitally, however, there is a marked change in tuberculation. Here the primary tubercle is considerably smaller and a second slightly smaller tubercle appears on each compound plate slightly adapical to the primary tubercle and closer to the adradial suture. In specimens less than about 10 mm in test diameter the secondary tubercle has not yet appeared, while in the largest specimens there is an additional tubercle, still smaller in size, that appears close to the perradial suture. Adorally the primary and secondary tubercles become separated so that a group of three plates united by the primary tubercle is followed by a group of two plates united by the secondary tubercle (Pl. 10, fig. 2). Above the ambitus there is also a marked change in tuberculation. Tubercle size rapidly diminishes adapically while at the same time more of each plate becomes covered with densely-packed miliary tubercles. At test diameters of less than about 10 mm only the top one or two tubercles per column are greatly reduced in size, but at larger sizes the most adapical three tubercles are greatly reduced. In this adapical region the ambulacra are simple.

INTERAMBULACRA. The interambulacral zones are surprisingly narrow for a pseudodiadematid, and in breadth measure 32–37% of the test diameter (mean = 33%; SD = 1·7; N = 12). There are seven interambulacral plates per column at 6·5 mm test diameter, eight to ten plates between 10 and 20 mm test diameter and 12 at 28 mm test diameter (Fig. 24). Adapical tubercles are small and rudimentary and much of each plate is covered in dense, uniform miliary tubercles. Towards the ambitus tubercles become markedly larger and there are usually two prominent primary tubercles in each column. Ambital primary tubercles are confluent and on these plates miliary tubercles are confined to a narrow adradial and interradial band. Immediately subambitally there is a distinct decrease in the size of the primary tubercle and secondary tubercles appear on each plate. At about 10 mm test diameter there are two large tubercles per plate subambitally, the primary tubercle and a slightly smaller secondary tubercle that lies slightly adapical and on the adradial side of the primary tubercle. A third, very much smaller tubercle may also be present perradially. In larger specimens the primary and secondary tubercles are equal in size and each plate has, in addition, a smaller perradial and adradial tubercle. Adorally all but the primary tubercle are lost from the plates. All tubercles are perforate and crenulate. Five or six ambulacral pores lie adjacent to an ambital interambulacral plate.

PERISTOME. The peristome is deeply sunken so that the adoral edges of the corona must be at about $\frac{1}{3}$ of the height of the test. The peristome is circular in outline and measures 31–40% of the test diameter (mean = 37%; SD = 2·8; N = 11). Buccal slits, broad and shallow and without a smooth rim, are present.

REMARKS. This species was first mentioned by Agassiz (1840*b*), who listed the names *Diadema lucae* and *Diadema rhodani* without description or illustration. In the same year Agassiz (1840*a*; actually published *after* 1840*b*) gave a brief diagnosis of these species together with figures. As later workers have pointed out, these two 'species' refer to juveniles and adults of the same

---

Fig. 24 Biometric data on *Allomma rhodani*: ● = specimens from Wilmington, Lower Cenomanian; □ = specimens from the 'Upper Greensand' of Warminster; ○ = specimen from the Middle Cenomanian of Chardstock.

species. Cotteau (1864), as first revisor, selected the name *D. rhodani* for this species and has been followed by all subsequent authors.

In 1856 Woodward published notes on British species of *Diadema*, in which the names *Diadema desori* Forbes and *D. pustulatum* Forbes were used for specimens from the Lower Cenomanian of Warminster and the Middle Cenomanian Basement Bed of Chardstock respectively. As Wright (1868) later pointed out, these two forms, like *Diadema lucae* and *D. rhodani*, are merely size variants and both are synonymous with *Allomma rhodani* (Agassiz).

The distinction between *Allomma rhodani* and *A. normaniae* Cotteau lies in the overall shape of the test and in the tuberculation. *A. normaniae* occurs in the Cenomanian Grey Chalk of Folkstone and is much more inflated, with uniformly curved sides and a flat top and base in profile. The change in tuberculation from a single large tubercle per plate to numerous small tubercles occurs very suddenly and this alone clearly distinguishes *A. normaniae* from *A. rhodani*.

Superorder **CAMARODONTA** Jackson, 1912

Family **GLYPHOCYPHIDAE** Duncan, 1889

Genus *GLYPHOCYPHUS* Haime, *in* d'Archaic & Haime 1853

Glyphocyphus radiatus (Agassiz 1836)

Pl. 11, figs 1–4; Pl. 40, fig. 4; Figs 25–27

1829 *Echinus radiatus* Hoeninghaus: Goldfuss: 124; pl. 40, fig. 13 [*non* Gmelin 1790].
1836 *Arbacia radiata* (Hoeninghaus) Agassiz: 190.
1840*b* *Echinopsis latipora* Agassiz: 9 [*nomen nudum*].
1840*b* *Echinopsis contexta* Agassiz: 9 [*nomen nudum*].
1840*b* *Echinopsis depressa* Agassiz: 9 [*nomen nudum*].
1847 *Echinopsis latipora* Agassiz; Agassiz & Desor: 50.
1847 *Echinopsis contexta* Agassiz; Agassiz & Desor: 50.
1847 *Echinopsis depressa* Agassiz; Agassiz & Desor: 50.
1850 *Echinopsis pusilla* (Roemer); Forbes, *in* Dixon: 340; pl. 25, fig. 30.
1850 *Glypticus Koninckii* Forbes, *in* Dixon: 340; pl. 25, fig. 31.
1853 *Glyphocyphus pulchellus* d'Archiac & Haime: 202.
1854 *Echinopsis pusilla* (Roemer); Forbes, *in* Morris: 78.
1856 *Glyphocyphus radiatus* (Hoeninghaus *in* Goldfuss) Desor: 103; pl. 17, figs 1–3.
1859 *Glyphocyphus radiatus* Desor; Cotteau & Triger: 158; pl. 28, figs 7–12.
1863 *Glyphocyphus radiatus* Desor; Cotteau: 535; pls 1127–8.
1870 *Glyphocyphus radiatus* Hoeninghaus; Wright: 121; pl. 29, figs 1, 2.
1878 *Echinopsis pusilla* (Roemer); Dixon & Jones: 340; pl. 25, figs 30, 31.
1894 *Glyphocyphus radiatus* Hoeninghaus; Lambert: 53.
1910 *Glyphocyphus radiatus* Hoeninghaus; Lambert: 193.
1943 *Glyphocyphus radiatus* (Hoeninghaus); Mortensen: 25; fig. 22.
1955 *Glyphocyphus radiatus depressus* (Agassiz); Szörényi: 177; pl. 1, figs 43–45.
1963 *Glyphocyphus radiatus* (Hoeninghaus); Cayeux: 23; fig. 12.
1966 *Glyphocyphus radiatus* (Hoeninghaus); Fell & Pawson: U415; fig. 310.1.

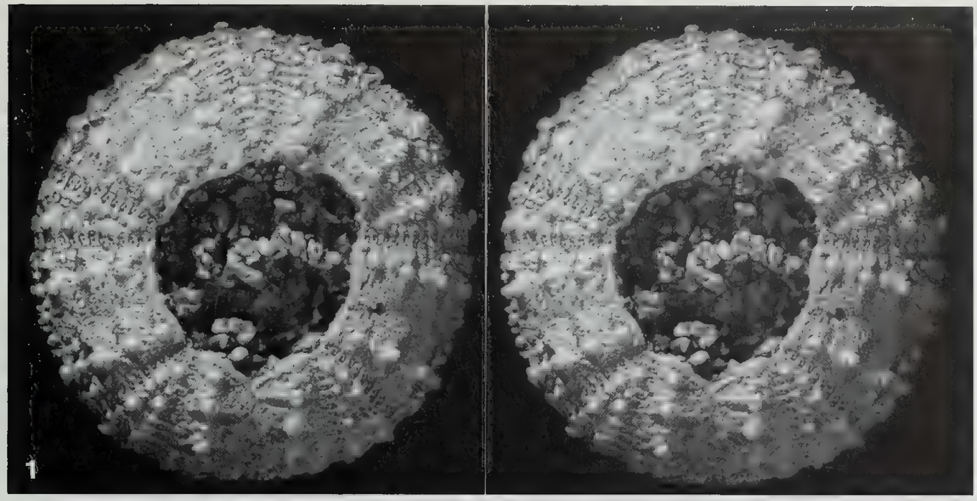
MATERIAL. Twenty-five well-preserved specimens from Wilmington (E.75580–3, E.76295–9, E.80046–61) were used in the biometric study. In addition a large number of specimens from the Upper Greensand of Warminster, the Grey Chalk of Dover and the Turonian Middle Chalk of Devon were examined.

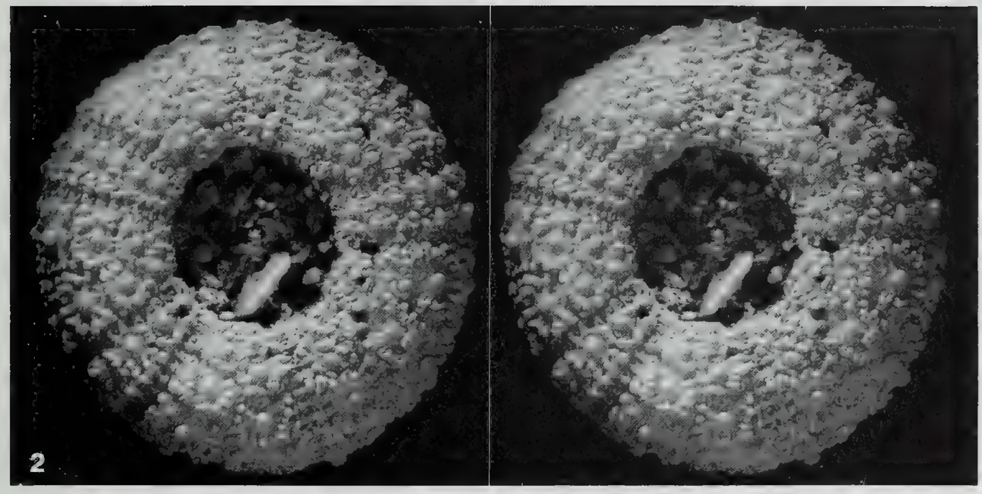
Plate 11

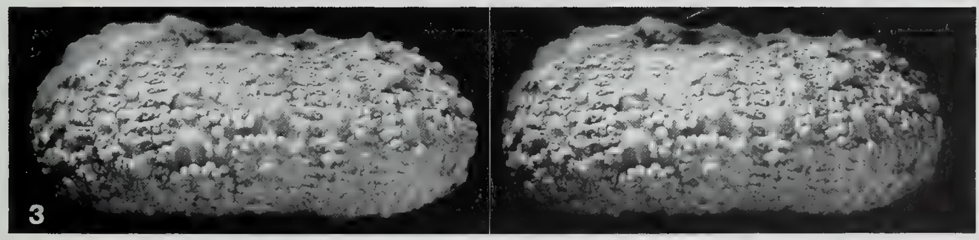
Glyphocyphus radiatus (Agassiz)

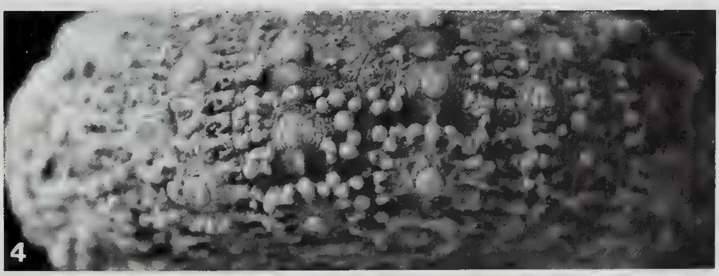
Figs 1, 2, 4 E.80050: 1, apical; 2, oral; 4, lateral. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 9).

Fig. 3 E.76257, lateral. As last (× 6).


1


2


3


4

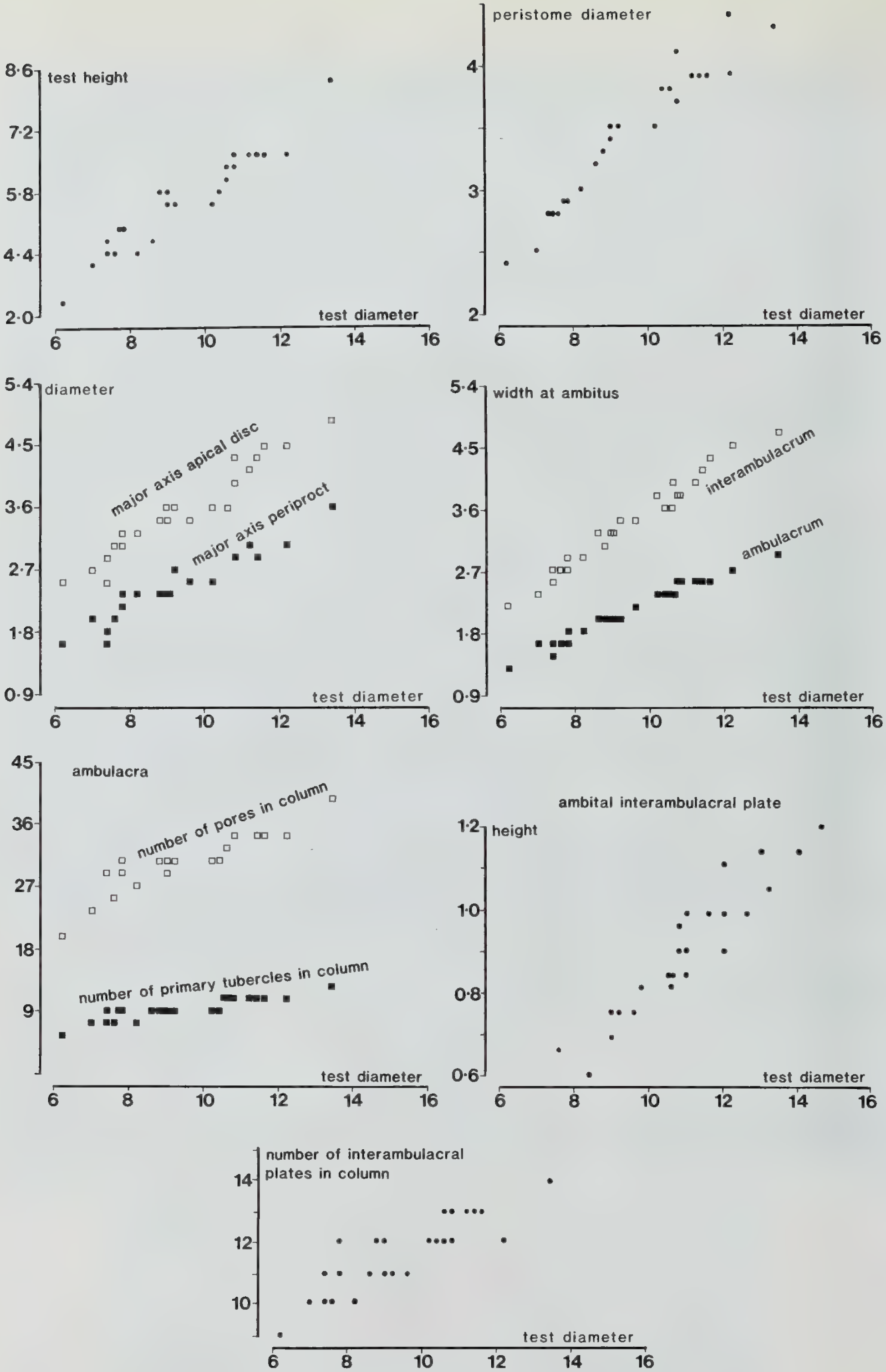


Fig. 25 Biometric data on *Glyphocyphus radiatus* from the Lower Cenomanian of Wilmington.

Stratigraphical occurrence and distribution. At Wilmington *G. radiatus* is not particularly common and only 9 stratigraphically located specimens were collected (E.80045–9, E.80052–5). These specimens come from the lower part of the Grizzle and the upper part of the Wilmington Sand from 231 to 550 cm below standard datum level. *G. radiatus* is also found in the Lower Cenomanian greensands of Chute Farm, Warminster, from the Cenomanian Grey Chalk of Dover and from the Lower Turonian of Sussex and south Devon.

Description. *SHAPE AND SIZE.* Tests range in size from 6·2 to 13·3 mm in diameter (mean = 9·5 mm; SD = 1·8; N = 25) and from 3·3 to 8·4 mm in height (mean = 5·6 mm; SD = 1·1; N = 24). In profile the test is rather flattened and the ambitus is slightly below mid-height. There is a broad, flat base and a smaller flat apical region. The test height is 53–65% of the diameter (mean = 59%; SD = 3·7; N = 24). In outline the test is circular. Ambulacral and interambulacral tubercles are similar in size and are relatively small and inconspicuous.

APICAL DISC. Plates of the apical disc are usually preserved in position and must have been firmly bound to the corona. Ocular plates are all exsert and the apical system is dicyclic (Fig. 26). Each ocular plate is broader than long and no ocular pore is visible from directly above. Genital plates are triangular in outline and have much the same width as ocular plates. A circular gonopore opens at the adambital point of the triangular genital plate. The madreporite (genital plate 2) is somewhat larger than the other genital plates and is obviously tumid, although it is still relatively small.

In outline the apical disc is distinctly oval, with the major axis in the plane passing through ambulacrum III and interambulacrum 5. The major axis of the apical disc is 34–42% of the test diameter (mean = 38%; SD = 2·1; N = 22) and the width of the apical disc (measured at right angles to the major axis) is 80–96% of the major axis (mean = 88%; SD = 4·4; N = 19). The periproct is egg-shaped, with the tapered end towards interambulacrum 5. The major axis of the periproct is 22–30% of the test diameter (mean = 27%; SD = 1·9; N = 19) and 63–76% of the major axis of the apical disc (mean = 69%; SD = 4·0; N = 19). The minor axis of the periproct is 78–97% of the major axis (mean = 84%; SD = 5·0; N = 19).

AMBULACRA. Ambulacral zones at the ambitus measure 20–29% of the test diameter (mean = 22%; SD = 1·6; N = 25). They taper only slightly adorally and adapically. Pores are arranged in a single straight line in each column and there is no concentration of pores adorally. All pores appear to be P_2-type partitioned isopores. The pore zone is slightly depressed and, at the ambitus, makes up about 25% of the ambulacral plate width. Ambulacral plates are compound in the acrosaleniid style, with a primary ambulacral tubercle overgrowing

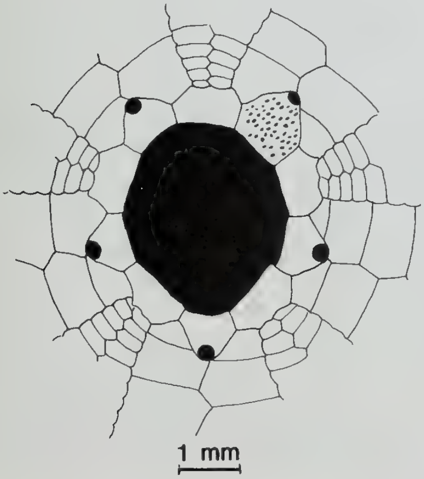


Fig. 26 Camera lucida drawing of the apical disc of *Glyphocyphus radiatus* (E.80045) from the Lower Cenomanian of Wilmington.

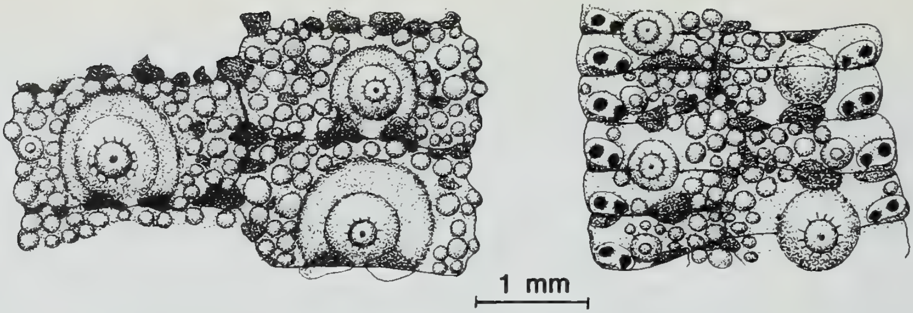


Fig. 27 Camera lucida drawings of ambital interambulacral plates (left) and ambulacral plates (right) in *Glyphocyphus radiatus* (E.80049) from the Lower Cenomanian of Wilmington.

two plates in every three (Fig. 27). In each ambulacral column there are 20 ambulacral pores and 6 primary tubercles at 6·2 mm test diameter, rising to 39 ambulacral pores and 13 primary tubercles at 13·3 mm test diameter (Fig. 25). Primary tubercles are relatively small and decrease in size gradually towards the apex. Miliary tubercles are abundant and each primary tubercle is separated from those above and below by a single irregular row of miliary tubercles on the single, unbound plate in each triad. Perradially there is a broad zone of dense miliary tubercles, two or three abreast. Small sutural depressions are present and are best developed immediately adoral to each primary tubercle but are also found where three sutures meet (Fig. 27).

INTERAMBULACRA. Interambulacral zones are a little less than twice as broad as ambulacral zones at the ambitus and in breadth are 34–38% of the test diameter (mean = 36%; SD = 1·0; N = 25). They are proportionally broader in larger individuals. At 6·2 mm test diameter there are nine interambulacral plates per column but this increases to 14 per column by 13·3 mm test diameter (Fig. 25). Plates at the ambitus are much broader than tall, so that plate height is on average only about 50% of the plate width. Each carries a single small and fairly inconspicuous primary tubercle; it lies slightly off-centre, being a little closer to the adradial suture than to the interradial suture. The tubercle has a relatively large mamelon with a tiny central perforation and a trace of feeble crenulation. The boss is small and the areole forms only 25–30% of the plate width. At the ambitus and adorally the primary tubercles are generally confluent, but above the ambitus a single row of miliaries is present adapical to the primary tubercles. On the adoral side of the boss of the primary tubercles there is a vertical ridge which becomes progressively stronger towards the adradial plate margin (Pl. 11, figs 3, 4) and on either side of this there is a prominent deep sutural pit. Miliary tubercles cover the remainder of the plate and these are densely-packed and uniform in size. On the adradial side of primary tubercles miliary tubercles are approximately two abreast whereas on the interradial side they are three abreast in all the larger individuals. Adorally, interambulacral plates carry a very much smaller secondary tubercle close to the adradial suture. Three ambulacral pores lie adjacent to each interambulacral plate at the ambitus. At the ambitus there are small sutural pits, generally occurring along the horizontal sutures and interradially where three sutures meet. The largest of them occur immediately beneath the primary tubercle (Fig. 27). Occasional tiny pits occur between the miliary tubercles in some specimens.

PERISTOME. The peristome is relatively small and circular in outline. In diameter it is 31–39% of the test diameter (mean = 36%; SD = 2·1; N = 24). It is hardly sunken. Buccal slits are exceedingly feeble and hardly indent the peristome margin.

REMARKS. The earliest description of this species was given by Goldfuss (1829) who used the manuscript name *Echinus radiatus* of Hoeninghaus for a specimen said to come from the 'Cretaceo margaceis' of Westphalia. Goldfuss placed this species within the group of regular echinoids characterized by having imperforate tubercles and acrosaleniid-style ambulacral plate compounding. Unfortunately, the name *Echinus radiatus* had already been coined by Gmelin

(1790) for an irregular echinoid, *Hemipneustes striatoradiatus* (Leske 1778). As Gmelin's name is a junior synonym and has never been used, whereas Goldfuss' *Echinus radiatus* has been the accepted name for this common Cretaceous echinoid for 160 years, an application is being prepared for submission to the ICZN to suppress Gmelin's application of the name.

The first record of the species in Britain was given by Forbes (*in* Dixon 1850) who appears to have given the name *Echinopsis pusilla* (Roemer) to the adapical view and the name *Glypticus Koninckii* to the inverted lateral view of the same specimen (E.12564). The early taxonomic confusion over this species was largely cleared up by Desor (1856) who provided an excellent description and figure. Full and detailed descriptions of this species were given by both Cotteau (1863) and Wright (1870) and the Wilmington population does not differ significantly in any details.

Order **TEMNOPLEUROIDA** Mortensen, 1943

Family **ZEUGOPLEURIDAE** Lewis, 1986

Genus ***GLYPTOCYPHUS*** Pomel, 1883

Glyptocyphus difficilis (Agassiz 1846)

Pl. 12, figs 1–4; Figs 28–30.

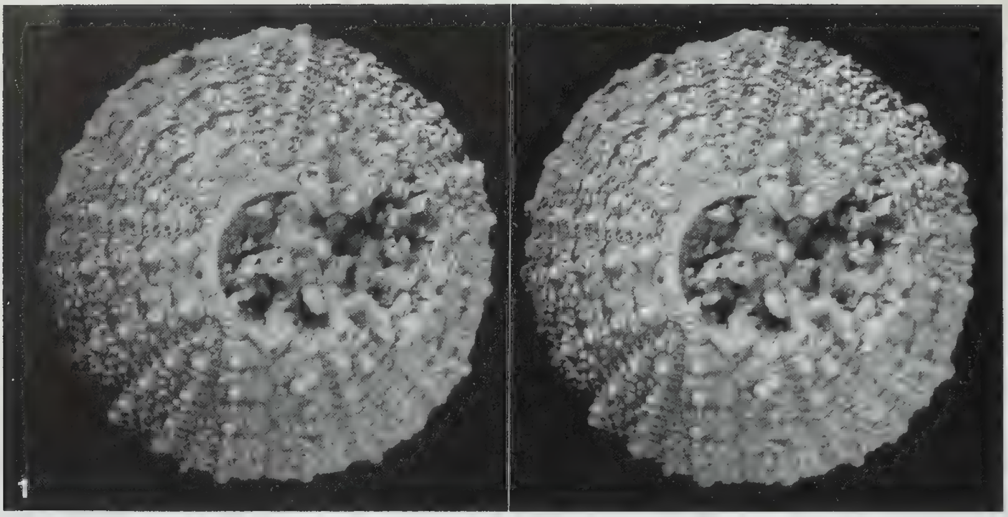
1840*b* *Cyphosoma difficile* Agassiz: 12 [*nomen nudum*].
1846 *Cyphosoma difficile* Agassiz; Agassiz & Desor: 352.
1848 *Diadema rotulare* M^{c}Coy: 420 [*nomen nudum; non* Agassiz].
1854 *Diadema M'Coyi* Forbes, *in* Morris: 76 [*nomen nudum*].
1854 *Diadema rotatum* Forbes, *in* Morris: 77 [*nomen nudum*].
1856 *Cyphosoma difficile* Agassiz; Woodward: Appendix p. 3.
1857 *Glyphocyphus difficilis* (Agassiz) Desor: 104.
1866 *Echinocyphus difficilis* (Agassiz) Cotteau: 708; pl. 1174, figs 1–8.
1866 *Echinocyphus rotatus* (Forbes) Cotteau: 711; pl. 1174, figs 9–19; pl. 1175, figs 1–4.
1870 *Echinocyphus difficilis* (Agassiz); Wright: 116; pl. 22, figs 1, 2, 4.
1883 *Echinocyphus difficilis* (Agassiz); Schlüter: 44.
1883 *Glyptocyphus difficilis* (Agassiz); Pomel: 87.
1910 *Glyptocyphus difficilis* (Agassiz); Lambert: 219.
1966 *Glyptocyphus difficilis* (Agassiz); Fell & Pawson: U399, fig. 279.1, 2.

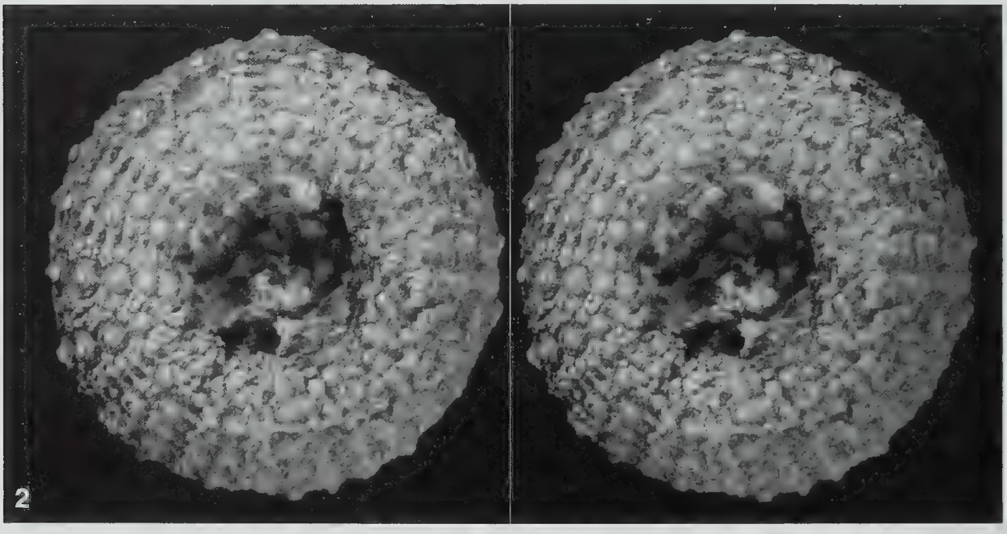
MATERIAL. Fourteen specimens of this species were collected from the quarry at Wilmington (E.80031–44), of which six were located accurately within the stratigraphical sequence. These 14 specimens were used in the biometric analysis. A number of other specimens from the Upper Greensand of Warminster were examined for comparison, including three (E.31460–1, E.79221) in which apical disc plating is preserved. The holotype, designated by Agassiz (1840*b*), is X79 which presumably is housed in the Neuchâtel Museum. A plaster cast of this specimen has been examined.

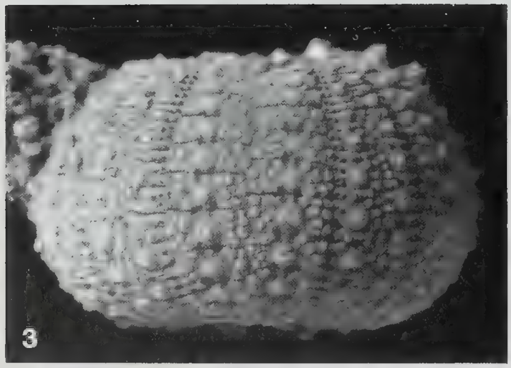
STRATIGRAPHICAL OCCURRENCE AND DISTRIBUTION. At Wilmington this species is found in the Grizzle and the upper part of the Wilmington Sands from 105 to 692 cm below standard datum level. It therefore comes from the Lower Cenomanian. The species is also relatively common in the Upper Greensand (Lower Cenomanian) of the Warminster region.

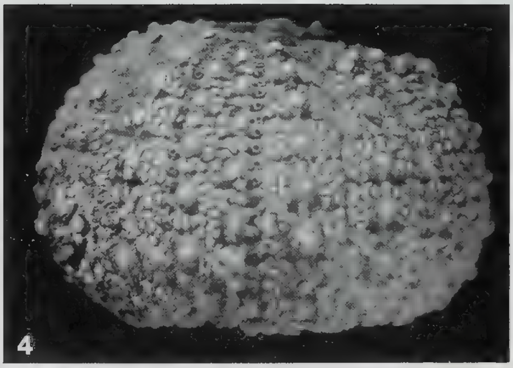
DESCRIPTION. *SHAPE AND SIZE.* Tests range in diameter from 6·0 to 10·8 mm (mean = 8·0 mm; SD = 1·6; N = 14) and are circular in outline. The test height is moderately variable; some specimens are distinctly flattened while others are more conical in profile (Pl. 12, figs 3, 4). The ambitus is at or very slightly below mid-height. Oral and apical surfaces are broad and flat in profile, the apical surface being usually slightly the smaller. The peristome is not noticeably sunken. Test height ranges from 2·9 mm to 5·5 mm and is 42–56% of the test diameter (mean = 49%; SD = 4·1; N = 14). Tubercles are small and inconspicuous, and ambulacral tubercles are slightly smaller than interambulacral tubercles.

APICAL SYSTEM. In outline the apical disc is approximately pentagonal and very slightly elongated in the anterior–posterior direction. The angles of the pentagon are interradial and


1


2


3


4

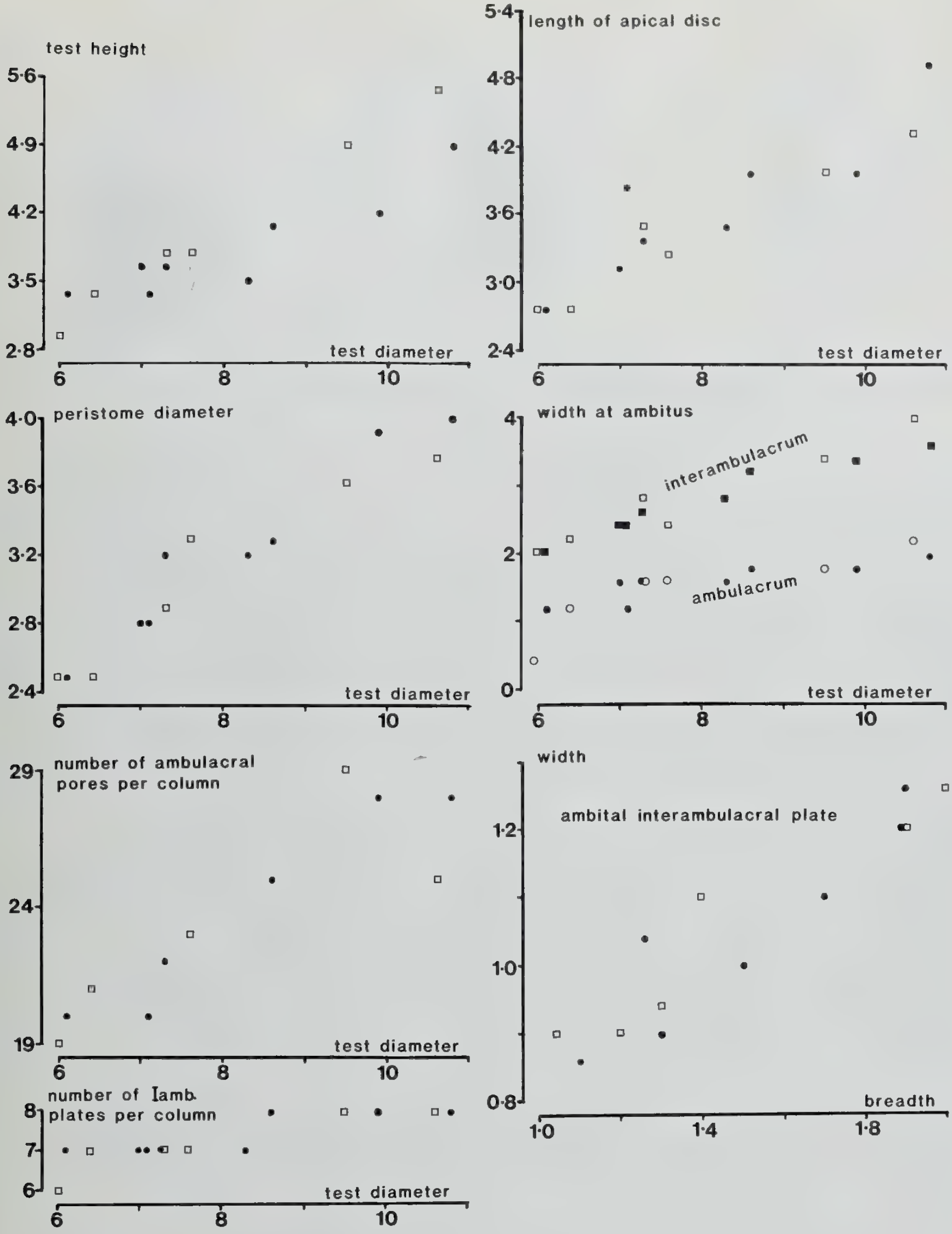


Fig. 28 Biometric data on *Glyptocyphus difficilis* from the Lower Cenomanian of Wilmington (○, □); solid symbols (●, ■) refer to variety *rotatus* (see p. 88).

Plate 12

Glyptocyphus difficilis (Agassiz)

Figs 1–3 E.80037: 1, apical; 2, oral; 3, lateral. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 6).

Fig. 4 E.88050, lateral. As last (× 8).

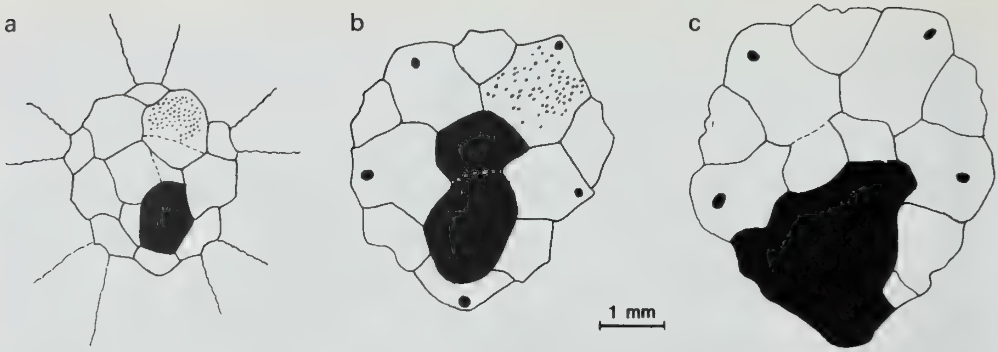


Fig. 29 Camera lucida drawings of apical discs of *Glyptocyphus difficilis* from the 'Upper Greensand' of Warminster. a, E.31461; b, E.31460; c, E.79221.

there is a distinct posterior interradial notch. The anterior–posterior axis measures 40–54% of the test diameter (mean = 45%; SD = 3·5; N = 14). The minor axis measures approximately 90% of the major axis. The plates of the apical system are preserved in three specimens from the Upper Greensand of Warminster (E.31460–1 and E.79221) (Fig. 29). Oculars II, III and IV are exert and are small, roughly v-shaped plates. Oculars I and V are larger and are insert, separating genital 5 from genitals 1 and 4. These posterior oculars are more elongate and are rather rectangular in outline. Ocular I borders onto the periproct but ocular V may be separated from the periproct by a thin suranal plate. Genital plates 1–4 are large and abut one another. They are polygonal, each with a gonopore near the interradial margin. The madreporite (genital plate 3) is only slightly larger than the other genital plates and the madreporic perforations are small and inconspicuous and are scattered over most of the plate surface. The posterior genital plate is small and U-shaped with a circular gonopore at its interradial point. There are, in addition, one to three suranal plates firmly incorporated into the apical disc, reducing the periproctal opening to a small oval hole lying posterior to the mid-point (Fig. 29). A large suranal plate lies anterior to the periproct, except in E.79221 where there appear to be two plates. An additional wedge-shaped plate may also be present separating genital 4 and ocular V from the periproct. The periproct is thus bordered by the anterior suranal plate(s), genital plate 1, ocular I, genital 5 and the latero-posterior suranal plate.

AMBULACRA. Ambulacral zones are relatively narrow, and in breadth measure 18–22% of the test diameter at the ambitus (mean = 20%; SD = 1·6; N = 14). The ambulacra taper adapically and, to a lesser extent, adorally. Ambulacral pores are arranged linearly; the pore zone is very weakly undulose at the ambitus where it forms 25–40% of the plate width. There are 19 ambulacral pores per column at 6·0 mm test diameter, rising to 28 at 10·8 mm test diameter (Fig. 28). Ambulacral plating is highly irregular, with a mixture of simple and compound plates. Primary ambulacral tubercles are equally irregular and may be present in one or both columns (Fig. 30). Primary tubercles are relatively small, perforate and non-crenulate. Each overlies two fused plates and there is a variable number of simple plates between succeeding compound plates. Ambulacral plate compounding is basically in the acrosaleniid style but occasionally demi-plates are found making echinoid-style compound plates. Miliary tubercles are present on simple ambulacral plates but no regular perradial tract of miliaries is developed. In the Wilmington population eight specimens have a single row of ambulacral tubercles in each ambulacrum while six specimens have a biserially alternate arrangement.

INTERAMBULACRA. The interambulacral zones are $1\frac{1}{2}$ to 2 times as broad as the ambulacral zones at the ambitus, where they measure 33–37% of the test diameter (mean = 35%; SD = 1·3; N = 14). There are six plates per column at 6·0 mm test diameter, rising to eight plates at 10·8 mm test diameter. At the ambitus, interambulacral plates are slightly broader than tall and the height of the plate is 63–85% of the plate breadth (mean = 71%; SD = 8·1;

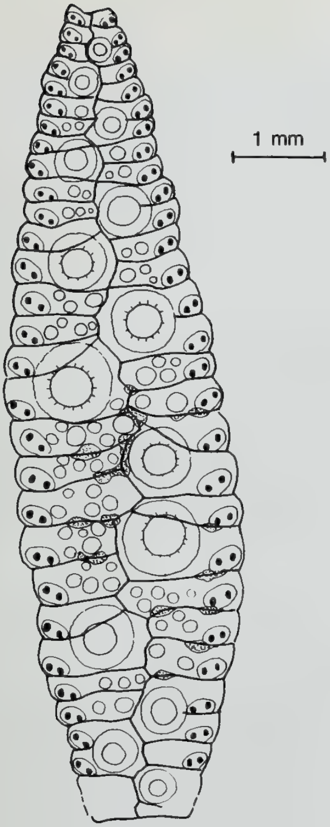


Fig. 30 Camera lucida drawing of one ambulacrum of *Glyptocyphus difficilis* (E.31467) from the Lower Cenomanian of Wilmington. Note the irregularity of tuberculation and the development of small pits.

N = 13). Each plate carries a single primary tubercle which is imperforate and shows only the faintest trace of crenulation. The mamelon has a relatively flat top and is large in proportion to the size of the boss (Pl. 12, figs 3, 4). The primary tubercle is surrounded on three sides by a scrobicular circle of 13 or 14 miliary tubercles. Adradially and perradially there may be a small number of additional miliary tubercles. The areole of primary tubercles is usually marked with feeble radiating ridges. Miliary tubercles are absent adoral of the primary tubercle, where instead two elongate sutural pits may be found; these pits are variably developed and are present only ambitally and adapically. Where sutural pitting is well developed, ambital plates give the appearance of overlapping one another. In larger specimens the three or so most adapical plates lack scrobicular tubercles and there is a prominent interradial naked zone. In these adapical plates the primary tubercles lie slightly towards the adradial edge of the plates. Three or four ambulacral pores lie adjacent to ambital interambulacral plates.

PERISTOME. The peristome is more or less circular in outline and its diameter is 36–44% of the test diameter (mean = 40%; SD = 2·1; N = 14).

REMARKS. The name *Cyphosoma difficile* was first used by Agassiz (1840*b*), where it appeared without accompanying description or figure. It was not validated until six years later when Agassiz (*in* Agassiz & Desor) provided a brief diagnosis for the species. The first record of this species in Britain was given by M^cCoy (1848), who unfortunately attributed the specimen to Agassiz' species *Diadema rotulare*. Forbes (*in* Morris 1854) must have recognized M^cCoy's error and gave the name *Diadema m'coyi* to the specimen, though without providing either description or figure. It was not until Woodward (1856) published his notes on British *Diadema* that the specimen was finally correctly attributed to Agassiz' species *Diadema difficile*. Wright (1870) gave a fairly good description of this species, although his interpretation of the apical disc plating is wrong.

Ambulacral tuberculation is irregularly developed in all specimens from Wilmington and it is possible to find specimens in which one ambulacral column has perfectly regular alternating ambulacral tuberculation while other ambulacral zones have a more irregular arrangement. Specimens with a regular ambulacral tuberculation were attributed by Cotteau (1866) to a separate species, *Echinocyphus rotatus*. However, because ambulacral tuberculation is so variably developed in the Wilmington population, I prefer to agree with Wright (1870) that *E. rotatus* is no more than a variety of *Glyptocyphus difficilis*.

Family **UNCERTAIN**

Genus ***COTTALDIA*** Desor, 1856

[=*Helodiadema* Mortensen, 1939]

DIAGNOSIS. An endocyclic euechinoid with wide interambulacral plates each bearing a row of small, minutely perforate tubercles; ambulacra with plates compounded in trigeminate acrosaleniid style: ambulacral pores arranged uniserially, no phyllodes: apical disc small, dicyclic, not caducous: peristome relatively small with feeble buccal slits: test subglobular to conical.

TYPE SPECIES. *Cottaldia benettiae* (König).

OTHER SPECIES. *Cottaldia rotula* Clark, *?C. sorigneti* Desor, *C. granulosa* (Goldfuss).

RANGE. Cretaceous (Albian–Cenomanian).

DISCUSSION. In recent years the genus *Cottaldia* has been placed within the family Arbaciidae Gray (e.g. Mortensen 1935, Fell & Pawson 1966). The Arbaciidae is a well-defined family whose living members are characterized by having (i) a stirodont lantern with arbaciid-style tooth plates (see Jensen, 1981); (ii) arbaciid-style ambulacral plate compounding; (iii) imperforate non-crenulate tubercles that increase in size noticeably subambitally; (iv) aboral tube feet that are specialized for gaseous exchange and are thus associated with conjugate ambulacral pores; (v) well-developed epistroma; (vi) prominent oral phyllodes; and (vii) large anal valve plates. Although the lantern is unknown, *Cottaldia* clearly is not an arbaciid because it has acrosaleniid-style ambulacral plate compounding, small but clearly perforate tubercles with traces of feeble crenulation, and no epistroma, phyllodes or ambulacral pores specialized for respiratory tube feet. The sole reason for placing *Cottaldia* in the Arbaciidae seems to be the general similarity of interambulacral tuberculation between *Cottaldia* and the true arbaciids *Codiopsis* and *Magnosia*. Although *Cottaldia* and *Magnosia* are superficially rather similar, the absence of any positive arbaciid character in *Cottaldia* shows that this is a convergent resemblance.

There are several other genera that bear considerably more similarity to *Cottaldia* than any arbaciid does. The genus *Helodiadema* was erected by Mortensen (1939) for the species *Cottaldia rotula* Clark because it has tubercles with a small but distinct mamelon perforation and traces of feeble crenulation, which supposedly distinguished it from *Cottaldia benettiae*. Yet the tubercles of *Cottaldia bennetiae* are unquestionably perforate and large tubercles do show traces of a feeble crenulation. The two genera are in my opinion synonymous and *Helodiadema* is here regarded as a junior synonym of *Cottaldia*. Interestingly, Mortensen (1939) placed *Helodiadema* in the Diadematoida because of its tubercle structure.

Micropedina Cotteau is another genus undoubtely very closely related to *Cottaldia*. The tuberculation is identical, or nearly so, and it is only in the details of the ambulacral plating that the genera can be distinguished. Both have uniserially arranged ambulacral pores and trigeminous plate compounding. However, in *Cottaldia* all three plates in a compound plate generally reach the perradial suture, although the middle of the three is always much larger than the other two (Fig. 33, p. 95). In *Micropedina*, according to Cotteau (1867), one of the three plates in each triad is occluded and does not reach the perradial suture. *Micropedina* is usually classified as a member of the Pedinoida on account of its perforate and apparently non-crenulate tubercles.

Dumblea Cragin also bears considerable resemblance to *Cottaldia*. Like *Cottaldia*, *Dumblea* has, on interambulacral plates, rows of small, equal-sized, minutely perforate tubercles which show traces of feeble crenulation. Ambulacral plate compounding is, however, more advanced than in either *Cottaldia* or *Micropedina*. In *Dumblea* the ambulacral pores are biserially arranged throughout and in each triad of plates both the upper and the lower plates are reduced and do not reach the perradial suture (a form of arbaciid plate compounding). *Dumblea* has been placed in the family Pseudodiadematidae in the *Treatise on Invertebrate Paleontology* (Fell & Pawson 1966).

The three genera most closely comparable with *Cottaldia* have therefore been classified within three different orders in the *Treatise*. They are clearly closely related and their current misclassification is largely because their detailed tubercle structure has been incorrectly reported. The fact that *Cottaldia* and its relatives retain a small but distinct tubercle perforation and traces of crenulation suggests that they evolved from ancestors with perforate, crenulate tubercles. The dicyclic apical system argues against them being diadematoids and the feeble crenulation might suggest that they are pseudodiadematids rather than pedinoids. Without knowing their lantern structure, however, it is impossible to be certain about their phylogenetic position. I have therefore left *Cottaldia* as *incertae sedis* until a specimen with lantern is discovered.

Cottaldia benettiae (König 1825)

Pl. 13, figs 1–3; Pl. 14, fig. 4; Figs 31–34

1825 *Echinus Benettiae* König: 2; pl. 3, fig. 35.
1849 *Echinus granulosus* Münster; Forbes: figs 1–4, 7–12 only [not figs 5, 6, = *Cottaldia granulosa*].
1858 *Cottaldia granulosa* Desor: 114; pl. 19, figs 1–3 [*non* Goldfuss].
1866 *Cottaldia Benettiae* (König) Cotteau: 789 [*partim*]; pl. 1193, figs 1–10 [not figs 11, 12, = *C. granulosa*]; pl. 1194, fig. 1 [not figs 2–9, = *C. granulosa*].
1866 *Cottaldia Sorigneti* Desor; Cotteau: 449; pl. 1195, figs 10–14.
1872 *Magnosia sequana* Bucaille: 189.
1873 *Cottaldia Benettiae* (König); Wright: 187; pl. 45, figs 1–3.
1883 *Magnosia sequana* Bucaille; Bucaille: 39; pl. 2, figs 3–7.
1940 *Cottaldia Benettiae* (König); Mortensen: 600; fig. 355a–f.
1963 *Cottaldia Benettiae* (Koenig); Cayeux: 21; fig. 11.

DIAGNOSIS. A subglobular species of *Cottaldia* with relatively few large tubercles per interambulacral plate arranged in a rather irregular row: miliary tubercles are much smaller than the primary tubercles and are not arranged into discrete rows between the rows of primary tubercles. In profile, interambulacral plates at the ambitus are more or less horizontal. Apical disc plates firmly bound to the corona.

NEOTYPE. König's original specimen came from the Cenomanian Upper Greensand of Chute Farm, Wiltshire but it is not present among the specimens of his collection housed in the British Museum (Natural History) and has presumably been lost. A specimen from the same locality and horizon, figured by Wright (1873: pl. 45, fig. 1), E.1595, is therefore here selected as **neotype**.

MATERIAL STUDIED. Thirteen more or less complete specimens form the basis of the biometric study, the neotype plus 12 specimens from Wilmington (E.16334, E.42304, E.76264–5, E.76328, E.76334, E.81084–9). A further four identifiable fragments (E.81090–3) were accurately located within the stratigraphical succession.

STRATIGRAPHICAL OCCURRENCE AND DISTRIBUTION. At Wilmington five specimens were accurately located within the succession. Of these, four were found in a narrow band near the top of the Grizzle, between 106 cm and 125 cm below standard datum level (Fig. 7). The fifth specimen, only a fragment but without doubt a member of this species, was found at about mid-height within the Wilmington Sands at 600 cm below standard datum level. *C. benettiae* comes from the Lower Cenomanian and is also known from the Cenomanian greensands of Wiltshire.

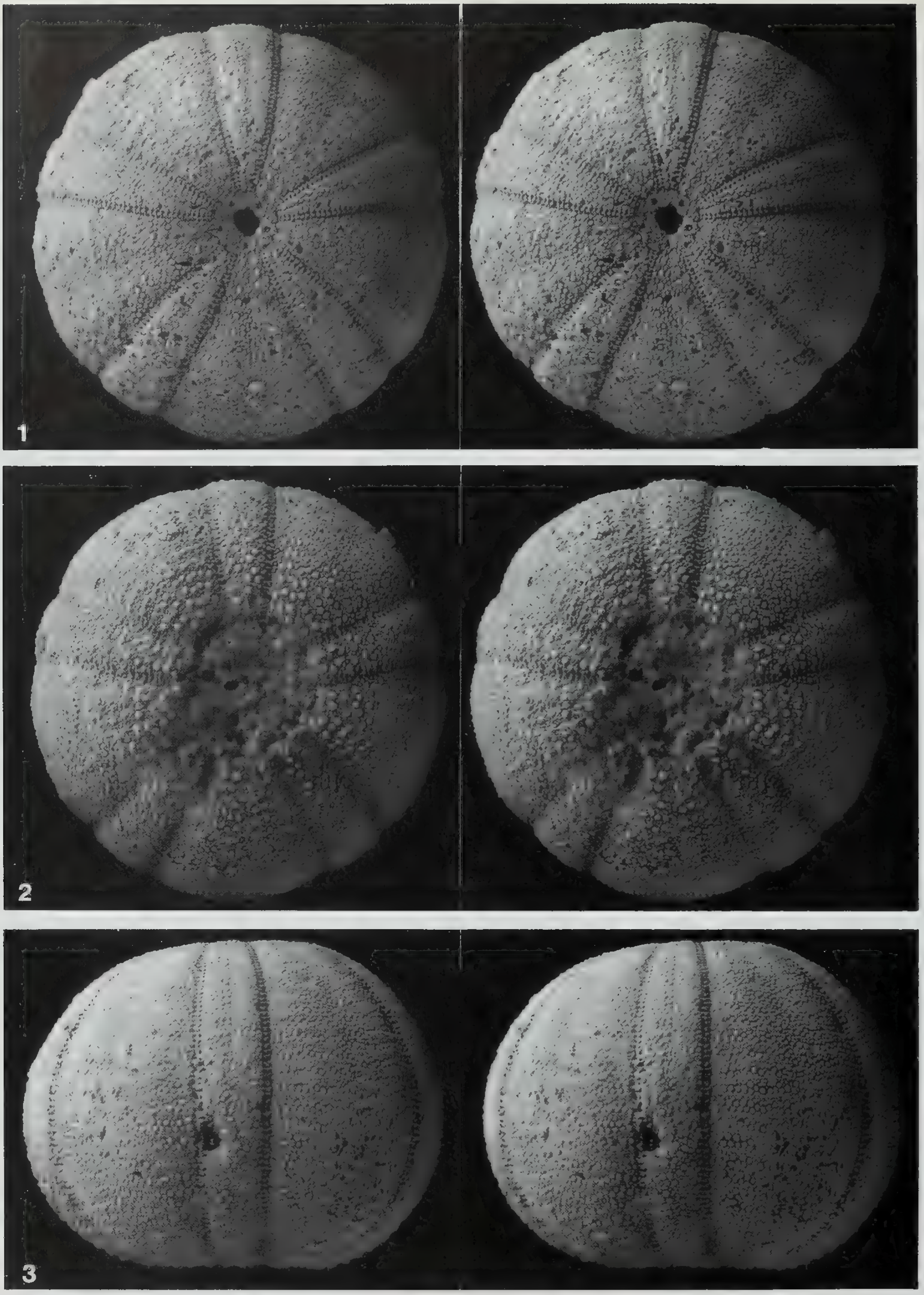


Plate 13
Cottaldia benettiae (König)
Figs 1–3 E.42304: 1, apical; 2, oral; 3, lateral. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 3·3).

DESCRIPTION. *SIZE AND SHAPE.* Tests range in size from 10 to 28 mm in diameter (mean = 16·0 mm; SD = 5·1; N = 13) and from 6·6 to 19·3 mm in height (mean = 11·5 mm; SD = 3·9; N = 13). The height of the test is 64–80% of the test diameter (mean = 71%; SD = 4·9; N = 13). The test is more or less circular in outline, although the interradial sutures are in general very slightly depressed. In profile there is a flat base and uniformly curved sides (Pl. 13, fig. 3). The ambitus lies more or less at mid-height.

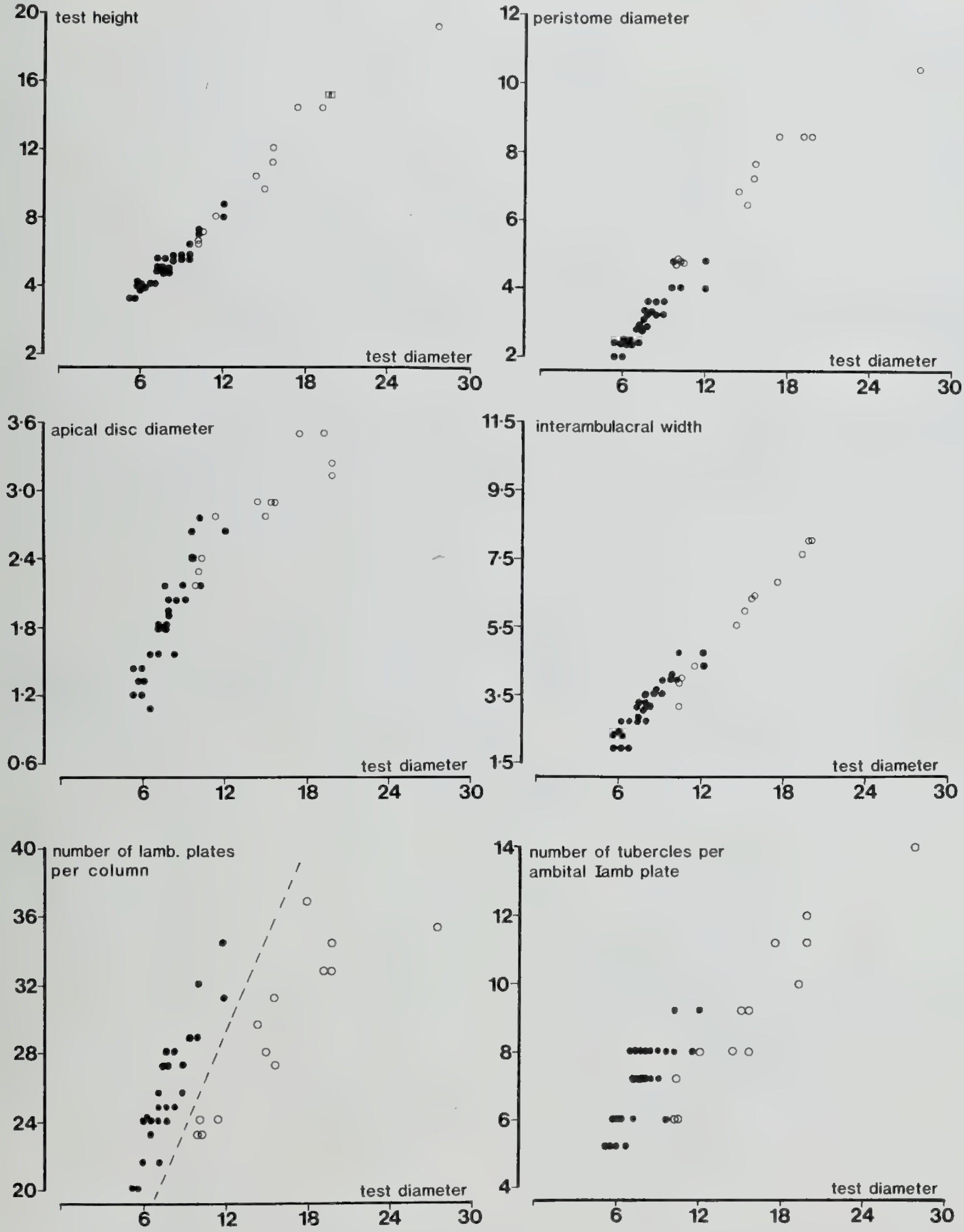


Fig. 31 Biometric data on *Cottaldia granulosa* (○) and *C. benettiae* (●) from the Lower Cenomanian of Wilmington.

APICAL SYSTEM. The plates of the apical disc are firmly bound to the corona and are usually preserved in place. The apical disc is small, only 16–24% of the test diameter (mean = 20%; SD = 2·9; N = 12), and circular in outline. The periproct is centrally positioned and irregularly oval in outline (Pl. 13, fig. 2). It is 8–11% of the test diameter (mean = 10%; SD = 1·0; N = 9). Ocular plates are all exsert and protrude slightly beyond the genital plates. They are covered in miliary tubercles and no ocular pore is visible from above. Genital plates are larger than the ocular plates, the madreporite being noticeably larger than the other four. Each is pierced by a large, centrally-placed gonopore; on the madreporite the gonopore is displaced towards the outer edge to accommodate the madreporic pores. Genital plates come to a small point interradially along their outer edge. Like the ocular plates, genital plates are covered in small miliary tubercles.

PERISTOME. This is circular in outline and forms 38–48% of the test diameter (mean = 45%; SD = 3·0; N = 11). It is more or less flush with the base of the test. Buccal slits are present but are only feebly developed.

AMBULACRA. These are straight and very slightly raised. At the apex they are about as broad as the interambulacra but at the ambitus they are only half as broad as the interambulacral zones. At the ambitus they are 16–21% of the test diameter (mean = 18%; SD = 1·6; N = 13). There are 18 compound ambulacral plates per column (54 ambulacral pores) at about 10 mm test diameter, rising to 31 compound plates (94 ambulacral pores) at about 28 mm test diameter. Each plate is broader than it is tall and is compound in the acrosaleniid style (Fig. 33c). Ambulacral pores, which are P_2 type (see Smith 1978), are linearly arranged. The pore zone is slightly sunken and forms 20–30% of the plate width at the ambitus. In the larger specimens the 6–9 ambulacral pores immediately adjacent to the peristome may be offset in triads. Each compound ambulacral plate has three or four larger tubercles on two of the three plates of the triad and some at least straddle the two plates (Fig. 33c). The third plate in each triad has a single row of miliary tubercles and is not linked to the other plates by tubercle overgrowth. Larger tubercles thus are arranged as a series of clusters. At the ambitus there are 2½ ambulacral pores adjacent to each interambulacral plate.

INTERAMBULACRA. The interambulacral zones are about twice as broad as the ambulacral zones at the ambitus, where they are 31–40% of the test diameter (mean = 38%; SD = 2·3; N = 13). At about 10 mm test diameter there are 23 plates per column but this increases to 35 plates per column at 28 mm test diameter. Individual plates are very wide and slightly kinked at about mid-length. Their height is only about 16–18% of their width. In all but the very largest specimens they have a single, slightly irregular row of large, equal-sized tubercles with tiny miliary tubercles interspersed both above and below. The primary tubercles, when well preserved, show a small but distinct perforation in the middle of the mamelon and

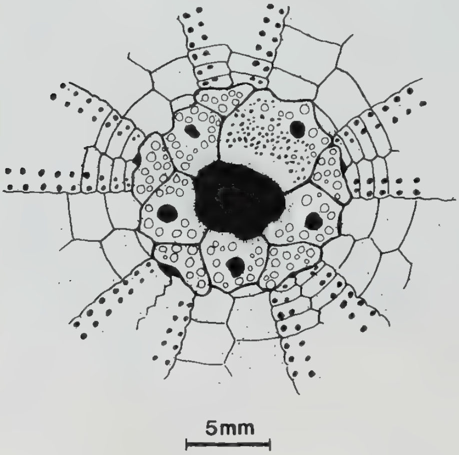


Fig. 32 Camera lucida drawing of the apical disc of *Cottaldia benettiae* (E.42304) from the Lower Cenomanian of Wilmington. Ambulacrum III to the top.

faint traces of crenulation around the mamelon. On each plate the primary tubercles are not arranged in a straight line but tend to be offset alternately above and below, particularly adradially. They show no apparent decrease in size towards the interradius. In large specimens the tubercles are arranged in two irregular rows. Interambulacral plates carry six primary tubercles at the ambitus in individuals approximately 10 mm in diameter, rising to 14 tubercles abreast at a diameter of 28 mm (Fig. 31). Interambulacral plates are more or less horizontal in profile, and there is only a very slight and gradual increase in tubercle size adorally.

DISCUSSION. *C. benettiae* is distinguished from *C. granulosa* on several features, of which the simplest are the number of interambulacral plates per column at any one size and the number of primary tubercles abreast on ambital interambulacral plates (Fig. 34). *C. benettiae* has significantly fewer interambulacral plates per column and also each plate bears fewer tubercles compared with *C. granulosa*. In *C. granulosa* the primary interambulacral tubercles are arranged in a line and decrease in size towards the interradius. Furthermore, the miliary tubercles are only slightly smaller than the primary tubercles and towards the interradius form a distinct row (Fig. 34). In *C. benettiae*, however, the primary tubercles are in a more irregular line, often displaced alternately to the top or bottom, and miliary tubercles are very much smaller and irregularly scattered. The apical disc of *C. benettiae* is generally preserved in place, whereas in *C. granulosa* it must have been more loosely bound to the corona and has not been preserved in any specimen I have seen. Whereas *C. benettiae* is subglobular in profile with the ambitus at mid-height, *C. granulosa* is more conical in profile (Pl. 14, fig. 3) and the ambitus occurs somewhat below mid-height. Finally, in side view the tuberculation of *C. granulosa* appears much denser and finer than that in a similar-sized *C. benettiae*, and the rows of tubercles of an interambulacrum form obtuse chevrons which point adorally in the interradius. In *C. benettiae* the rows of tubercles are more widely spaced and run more or less horizontally. *C. benettiae* apparently grew to a considerably larger size than *C. granulosa*. All these differences are consistent and clearly distinguish the two species.

Cottaldia granulosa (Goldfuss 1829)

Pl. 14, figs 1–3; Figs 31, 33a, b, 34a.

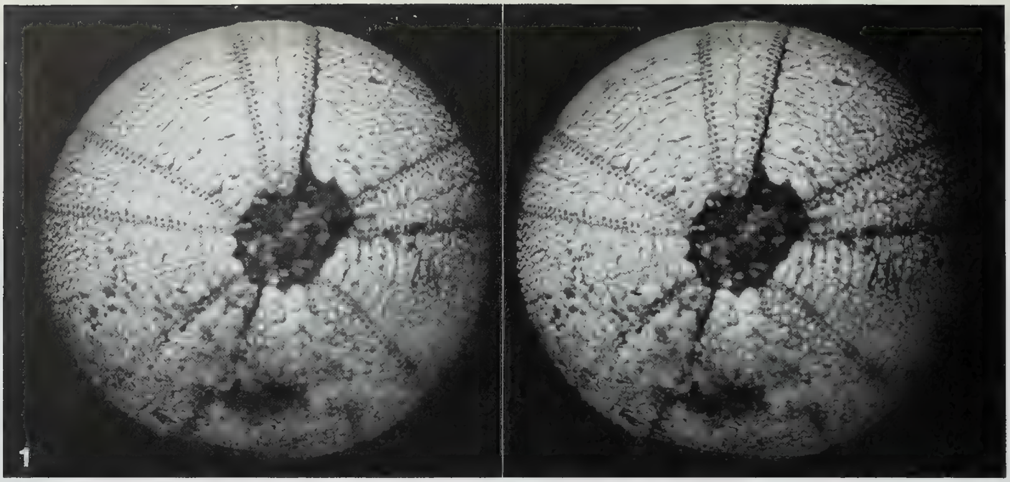
1829 *Echinus granulosus* Münster [Ms]; Goldfuss: 125; pl. 49, fig. 5.
1847 *Arbacia granulosa* Münster; Agassiz & Desor: 52.
1847 *Arbacia conica* Agassiz; Agassiz & Desor: 52.
1849 *Echinus granulosus* Münster; Forbes: 1 [*partim*]; pl. 1, figs 5, 6 [not figs 1–4, 7–12, = *C. benettiae*].
1866 *Cottaldia Benettiae* (Koenig); Cotteau: 789 [*partim*]; pl. 1193, figs 11, 12; pl. 1194, figs 2–4, ?7, 8.

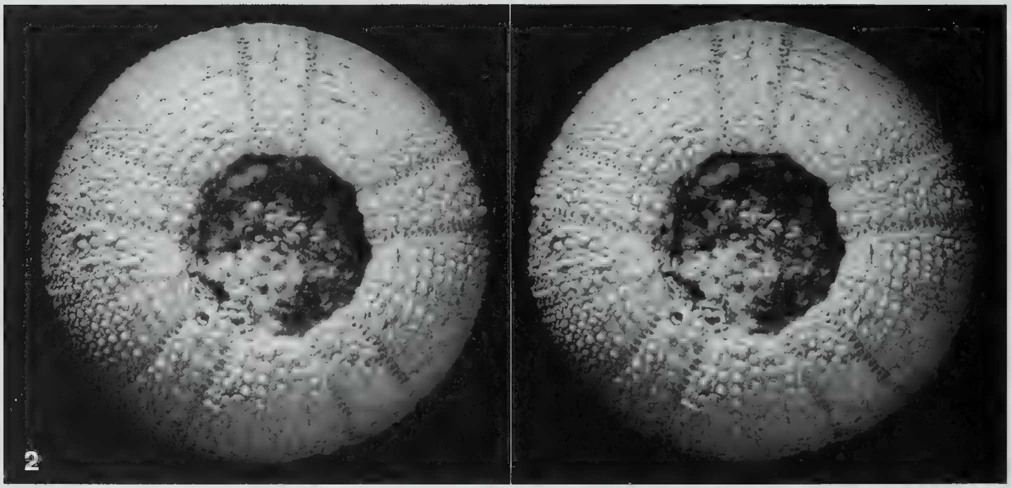
DIAGNOSIS. A conical species of *Cottaldia* with many interambulacral plates per column, each with numerous small tubercles arranged linearly and decreasing in size interradially. Miliary tubercles only slightly smaller than primary tubercles and also generally arranged linearly. Apical disc loosely bound to the corona and readily lost. In profile the rows of interambulacral tubercles form obtuse chevrons which point adorally.

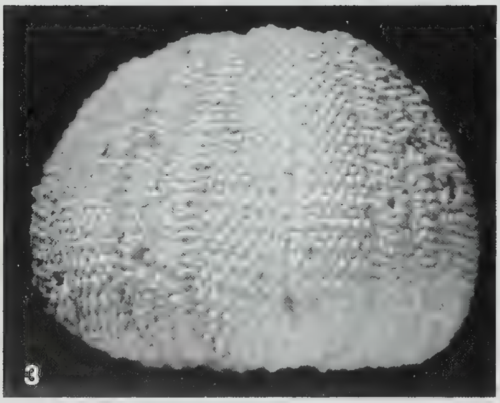
MATERIAL. Twenty-nine well-preserved individuals (E.76335, E.81094–121) from Wilmington were used for the biometric study. Of these, 11 were located accurately within the stratigraphical succession. A further two identifiable but incomplete tests also have accurate stratigraphical data.

STRATIGRAPHICAL OCCURRENCE AND DISTRIBUTION. At Wilmington *C. granulosa* occurs from 462 cm to 130 cm below standard datum and is apparently scattered through the upper part of the Wilmington Sands and the lower part of the Grizzle. It therefore comes from the Lower Cenomanian. Elsewhere in Britain this species is found in the Lower Cenomanian greensands of Warminster and the Lower Cenomanian of the south Devon coast.

DESCRIPTION. *SIZE AND SHAPE*. Specimens range in size from 5·6 to 12·2 mm in diameter (mean = 8·0 mm; SD = 1·7; N = 29) and from 3·1 to 8·5 mm in height (mean = 5·1 mm;







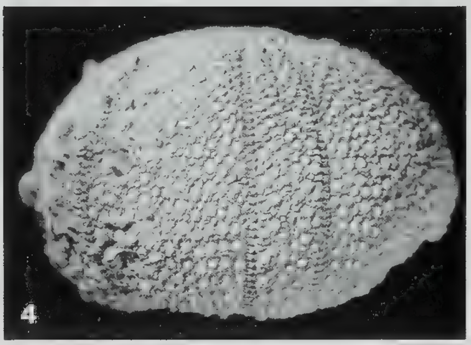


Plate 14

Cottaldia granulosa (Goldfuss)

Figs 1, 2 E.76335: 1, apical; 2, oral. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 5·3).

Fig. 3 E.81109, lateral. As last (× 8).

Cottaldia benettiae (König), juvenile

Fig. 4 E.81089, lateral. As last (× 6). Compare with fig. 3.

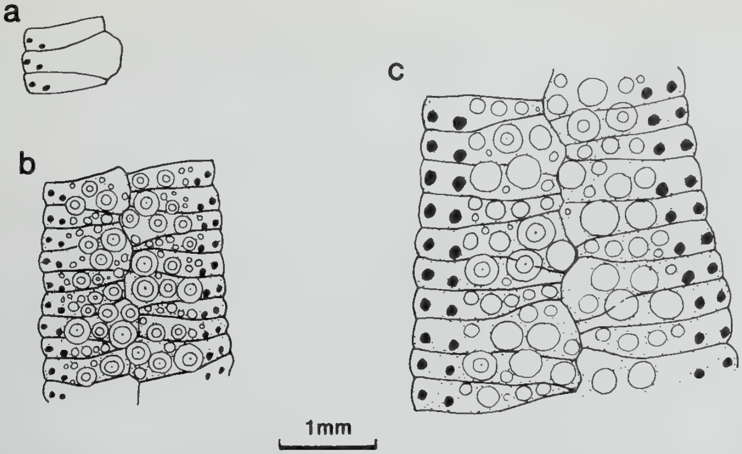


Fig. 33 Camera lucida drawings of ambulacral plate compounding in *Cottaldia*; a, b, *C. granulosa* (E.81118); a, one triad; b, ambital plating. c, *C. benettiae* (E.76334), ambital plating.

SD = 1·3; N = 28). The test is relatively tall, its height being 55–74% of the diameter (mean = 64%; SD = 4·4; N = 29). The base is broad and flat and the corona is roughly conical in shape. The ambitus is situated relatively low down, at about one-third of the test height. In outline the test is circular.

APICAL DISC. No specimen is preserved with any of the apical disc plates in position and they must have been only loosely bound to the corona. The diameter of the apical disc is 17–27% of the test diameter (mean = 23·0%; SD = 3·7; N = 28). It is circular in outline and has shallow, poorly-developed buccal slits. The peristome is proportionally larger in juveniles.

AMBULACRA. These are straight and at the ambitus are approximately half as broad as the interambulacral zones. At the ambitus, ambulacral width is 15–23% of the test diameter (mean = 19%; SD = 2·5; N = 27). Ambulacral pores are arranged uniserially from apex to peristome and the poriferous zone forms about 25% of the ambulacral plate width. Ambulacral plates are compound in the acrosaleniid style (Fig. 33). Three plates make up each compound ambulacral plate, of which the middle plate is always the largest. Generally all three plates in each triad reach the perradial suture, but occasionally one or other of the smaller plates may be occluded and not quite reach the perradius. There are 11–12 plates (34–36 ambulacral pores) per column at 5·6 mm diameter, rising to 18–19 plates (58 ambulacral pores) at 12·2 mm test diameter (Fig. 31). Each compound plate carries one or sometimes two larger tubercles together with a number of smaller tubercles arranged much as in *C. benettiae*. Each interambulacral plate lies opposite 1½–2 ambulacral pores at the ambitus.

INTERAMBULACRA. The interambulacral zones are about twice as broad as the ambulacra at the ambitus (29–44%; mean = 39%; SD = 3·7; N = 28). At 5·6 mm test diameter there are 20 interambulacral plates per column, rising to 34 at 12·2 mm test diameter. Individual plates are very wide and carry a single line of primary tubercles which decrease in size slightly towards the interradius. Miliary tubercles are only slightly smaller than the primary tubercles and are also aligned into a row above the primary tubercles. These miliary tubercles abut on one another towards the interradius; the test tuberculation thus consists very characteristically of alternating rows of primary and miliary tubercles (Fig. 34). Primary tubercles have a small but distinct central perforation when well preserved. In side view the lines of tubercles are perfectly straight and slope adorally towards the perradius, so that the two columns together appear to have tuberculation arranged in an obtuse chevron which closes adorally (Pl. 14, fig. 3). At 5·6 mm test diameter there are five primary tubercles per plate, but this rises to nine tubercles by 12 mm test diameter (Fig. 31).

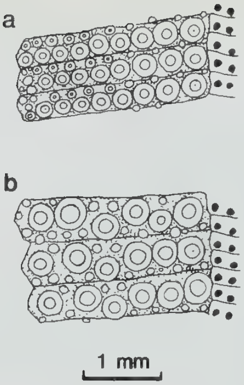


Fig. 34 Camera lucida drawings of ambital interambulacral plates of *Cottaldia*: a, *C. granulosa*, E.76335; b, *C. benettiae*, E.81089. (Both specimens are of approximately the same diameter).

DISCUSSION. In the past this species has not been distinguished from *Cottaldia benettiae*. The specimen figured by Goldfuss (1829), under the manuscript name *Echinus granulosus* of Münster, is conical and has no apical disc plating preserved. This appears to be identical to the specimens described here and is very different in shape from the specimens figured by König (1825) and Wright (1874) as *Cottaldia benettiae*. Previous workers such as Cotteau (1866) and Wright (1874) have synonymized this species with *C. benettiae* König, but the two can be readily distinguished on the basis of differences in interambulacral plating (Fig. 31). The reasons for separating these two species have already been discussed under *C. benettiae* (p. 93).

Cohort **IRREGULARIA** Latreille, 1825

Order **HOLECTYPOIDA** Duncan, 1889

Family **DISCOIDIDAE** Lambert, 1900

Genus ***DISCOIDES*** Parkinson, 1811

Discoides subuculus (Leske 1778)

Pl. 15, figs 1–3; Pl. 19, fig. 1; Figs 35–36, 37b–d, 38.

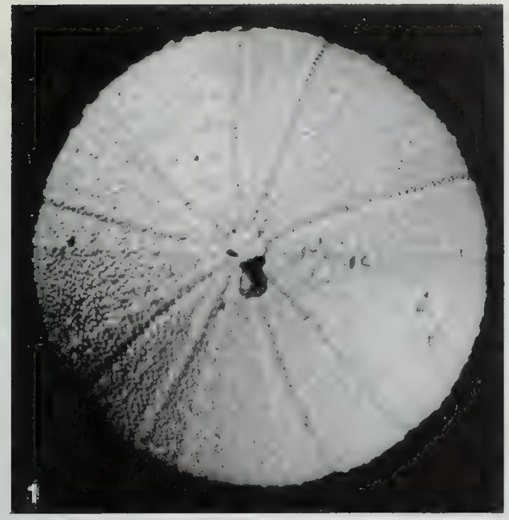
1734 *Discoides subuculus* Klein: 26; pl. 14*l*, *m* (pre-Linnaean).
1778 *Echinites subuculus* Leske: 171; pl. 14*m*, *n*, *o*
1873 *Discoidea subuculus* Klein; Wright: 200; pl. 45, figs 4–6 (q.v. for prior synonymy).
1955 *Discoidea subucula* Klein (*in* Leske); Szörényi: 187; pl. 4, figs 7, 8, 10–17, 21.
1966 *Discoides subucula* (Leske); Wagner & Durham: 444; fig. 330.3

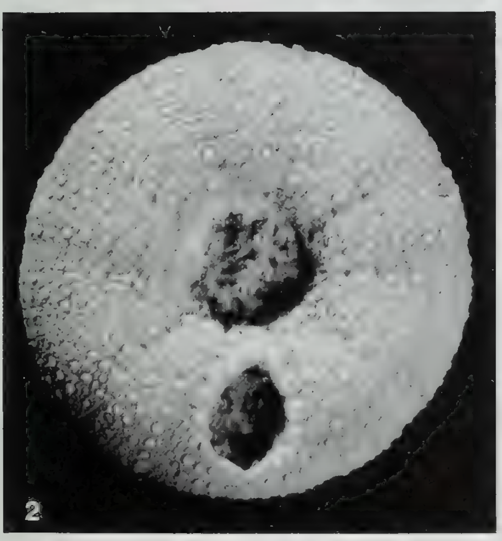
MATERIAL. Several hundred examples of this species were collected loose at Wilmington, 64 well-preserved specimens of which (E.82648–712) were used in the biometric analysis and are described below. A further 261 specimens were collected *in situ* (Fig. 7, pp. 18–19).

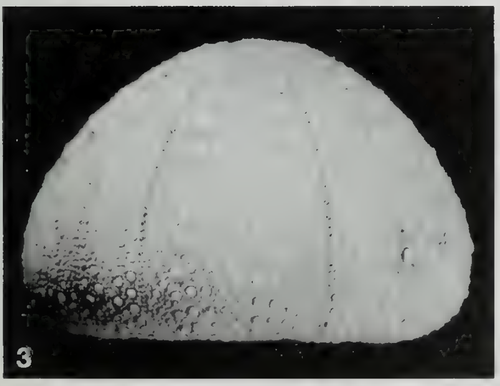
STRATIGRAPHICAL OCCURRENCE AND DISTRIBUTION. At Wilmington this species occurs throughout the lower part of the succession up as far as the base of the Wilmington Limestone. It is therefore restricted to the Lower Cenomanian; it is a common species in Lower Cenomanian sand facies of south-western England.

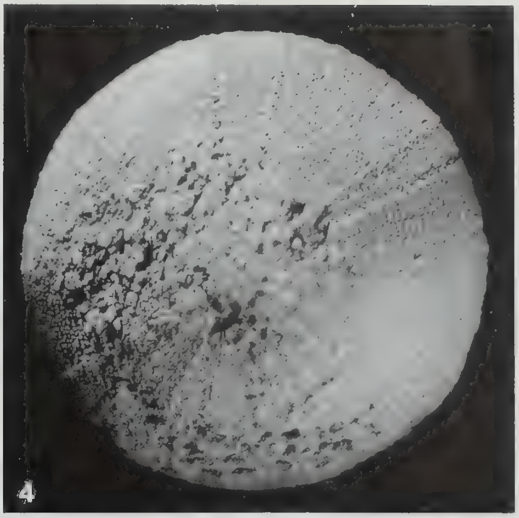
Plate 15
Discoides subuculus (Leske)
Figs 1–3 E.81269: 1, apical; 2, oral; 3, lateral. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 6). See also Pl. 19, fig. 1.

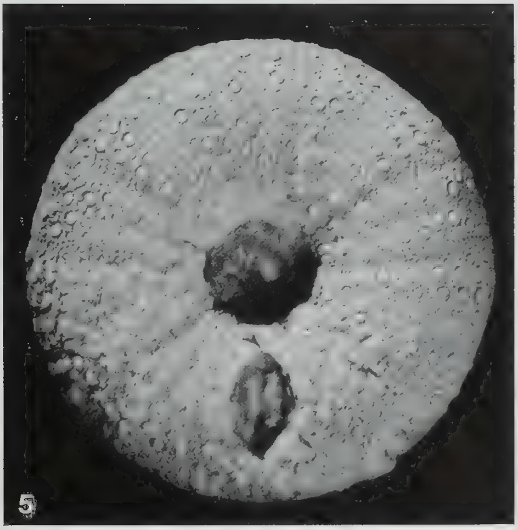
Discoides inferus (Desor)
Figs 4–6 E.80897: 4, apical; 5, oral; 6, lateral. As last (× 6). See also Pl. 19, fig. 2.

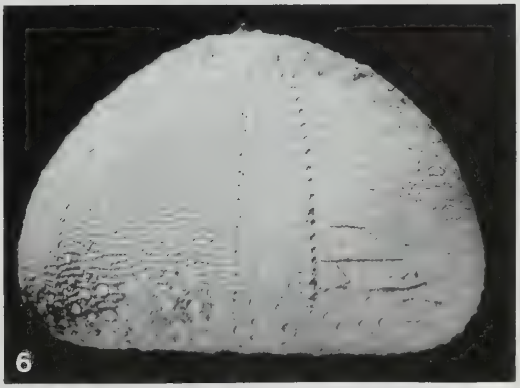

1


2


3


4


5


6

DESCRIPTION. *SIZE AND SHAPE.* Tests range in diameter from 3·2 to 11·5 mm (mean = 8 mm; SD = 1·8; N = 64) and in height from 2·3 to 6·9 mm (mean = 4·6 mm; SD = 1·2; N = 64). The test is circular to subpentagonal in outline, with the angles of the pentagon at ambulacra. In profile the test is generally conical, but in the flatter forms it is more hemispherical. The tallest point of the test is central and coincides with the apical disc. The ambitus is relatively low, between a quarter and a third of the height above the base.

APICAL SYSTEM. The apical disc lies centrally at the apex of the test. It is relatively small, only 7–10% of the test diameter (mean = 9%; SD = 1·1; N = 43). There are five genital and five ocular plates. The madreporite is larger than other genital plates (Fig. 36b) and is in contact with the other four genital plates. In some specimens the madreporic perforations are not

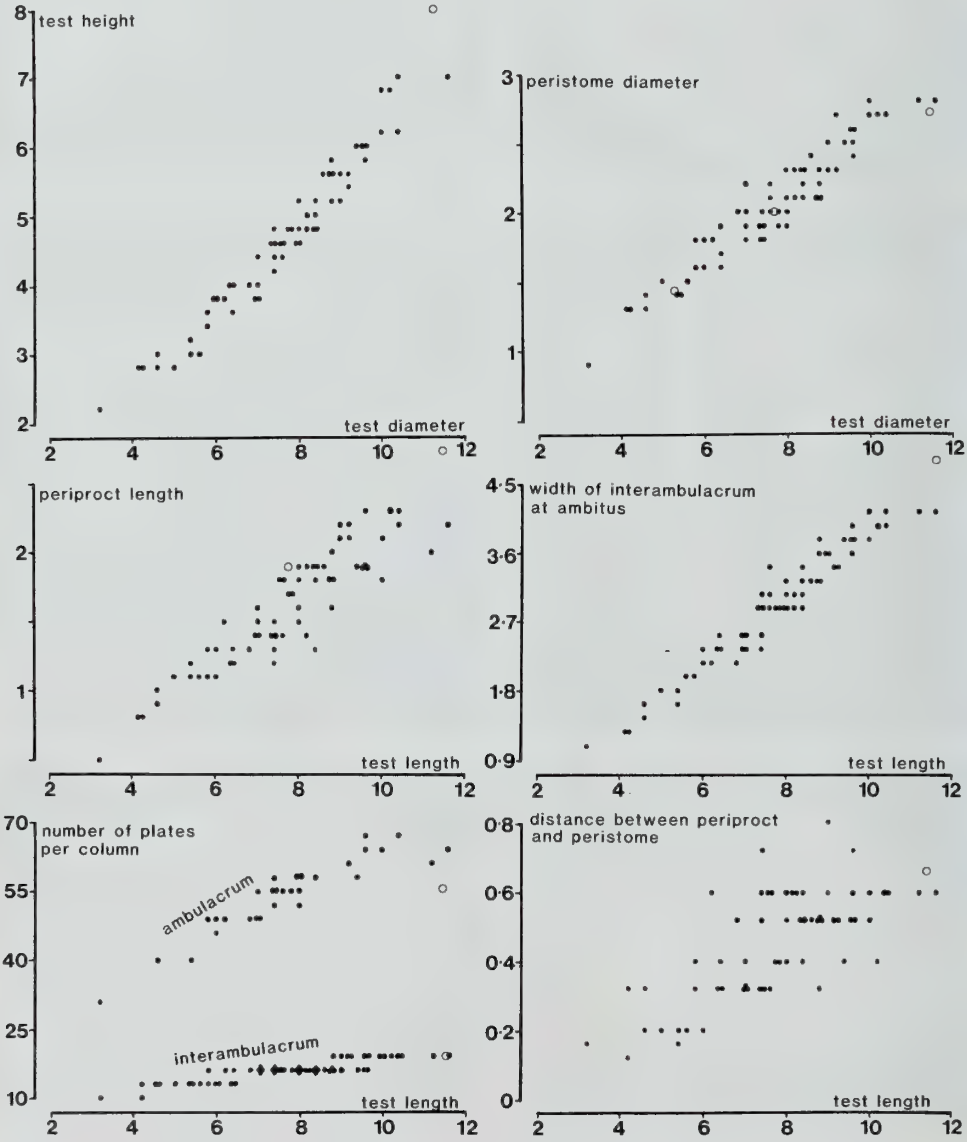


Fig. 35 Biometric data on *Discoides subuculus* (●) and *D. inferus* (○) from Wilmington.

confined to genital 2 but can also be found in the adjacent regions of other genital plates. There are four gonopores, the posterior genital plate being imperforate. The gonopores generally appear when the test has reached a diameter of around 5–6 mm, although exceptionally they are present in tests as small as 4 mm in diameter. There is no evidence of sexual dimorphism. Ocular plates are small and not in contact with one another.

AMBULACRA. These are relatively narrow, measuring 12–20% of the test diameter (mean = 16%; SD = 3·5; N = 64). They are widest just above the ambitus and taper gently adapically. Ambulacral pores are arranged in a straight line and are entirely undifferentiated from apex to peristome. All ambulacral pores are P_2-type partitioned isopores and there are neither petals nor phyllodes. The pore zone forms only a small part of the ambulacral plate width, about 10–15% of the plate width at the ambitus. There are about 30 ambulacral plates per column at a test diameter of 3·2 mm, rising to 63 by 10 mm test diameter (Fig. 35). Ambulacral plates are short and elongate at the ambitus, where the ambulacral pores are most closely packed. Adorally the plates become relatively a little taller and ambulacral pores become a little less crowded. All ambulacral plates are simple, in that there are no tubercles that overgrow and unite two or more plates. Adapically, ambulacral plates each bear one or more small tubercles which alternate in position in successive plates. At the ambitus and adorally, plates are arranged in triads and a form of pseudocompounding is found. Every third plate is enlarged and carries a primary ambulacral tubercle. One of the two other plates in each triad is occluded from the perradial suture (Fig. 36a).

INTERAMBULACRA. These are a little more than twice the width of the ambulacra, measuring 31–43% of the test diameter (mean = 37%; SD = 3·0; N = 64). There are 11 interambulacral plates per column in a specimen 3·2 mm in diameter, rising to 20 in specimens

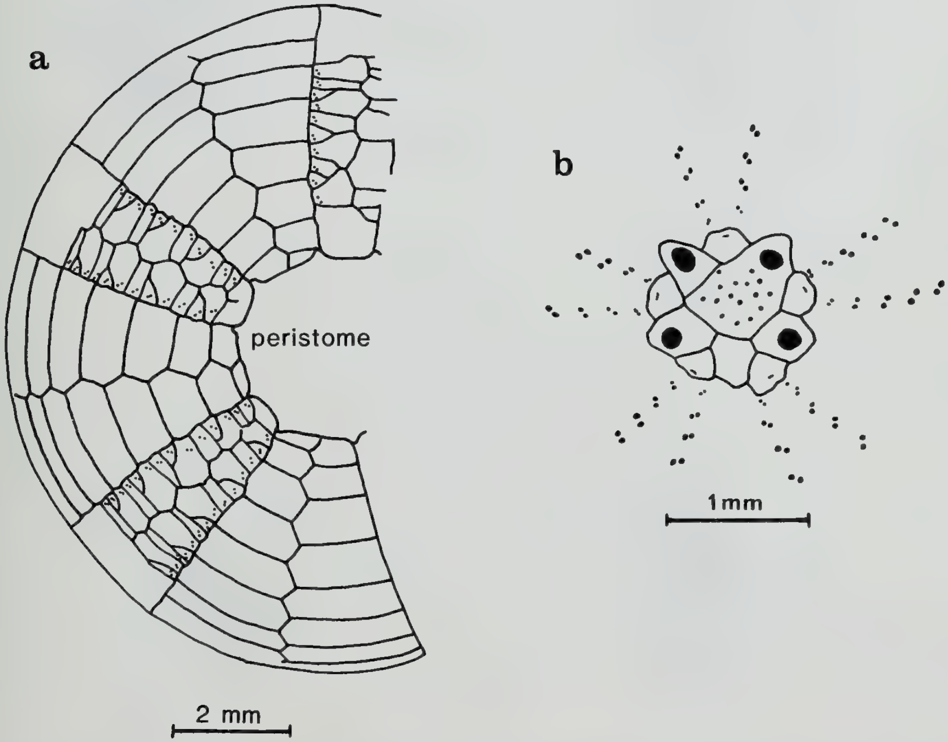


Fig. 36 Camera lucida drawings of (a) oral plating, and (b) apical disc in *Discoides subuculus* (E.82717) from the Lower Cenomanian of Wilmington.

10–11·5 mm in diameter (Fig. 35). The interambulacral plates are considerably wider than tall; at the ambitus mean plate height is 24% of plate width (SD = 1·5; N = 10). Each interambulacral plate has a small primary tubercle at the centre and up to two other secondary tubercles of much the same size at the ambitus. A further two tubercles, very much smaller than the three principle tubercles, may be present towards the adradial edge of the plate. These are not aligned with the other tubercles. There are about four ambulacral pores opposite each interambulacral plate at the ambitus, but only three subambitally.

PERISTOME. This is circular in outline and slightly sunken and is 25–31% of the diameter (mean = 27%; SD = 2·1; N = 64). There are distinct gill slits and although these are shallow they are sharply defined. No concentration of ambulacral pores or dense tuberculation is developed around the peristome.

PERIGNATHIC GIRDLE. There are well-developed internal auricles, which remain unfused perradially. Internally there are also 10 well-developed ridges lying at the adradial edge of interambulacral columns; they are present only on the oral surface and are best developed adambitally.

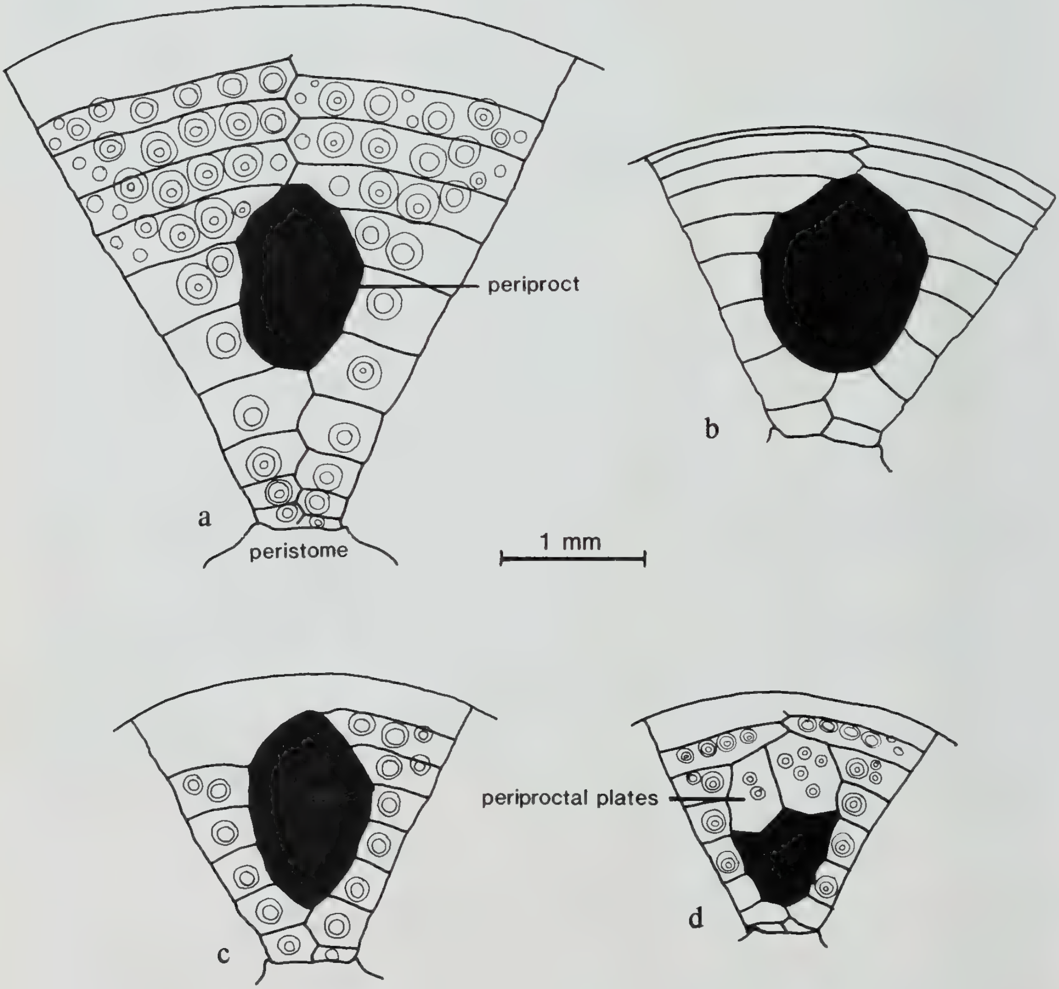


Fig. 37 Camera lucida drawings of the oral plating in the posterior interambulacram of *Discoides* from Wilmington. a, *D. favrinus*, E.80855: b–d, *D. subuculus*; b, E.81271; c, E.82718; d, E.82716.

PERIPROCT. This lies close to the peristome on the oral surface. It is lensoidal in outline, slightly more pointed adorally than adambitally. Its length is 15–24% of the test length (mean = 21%; SD = 2·4; N = 64), and its width is 53–91% of its length (mean = 77%; SD = 16·8; N = 64). The distance separating the peristome and periproct is 2·4–9·7% of the test length (mean = 6%; SD = 1·6; N = 61) and separating the periproct from the posterior of the test 0–10% (mean = 4%; SD = 1·9; N = 60). The periproct lies closer to the posterior edge of the test in juveniles and two interambulacral plates in each column separate the peristome and periproct. Two large periproctal plates are occasionally preserved, covering the adambital part of the opening (Fig. 37d). These have previously been described by Holmes (1935).

TUBERCULATION. Apical tubercles are noticeably smaller than adoral tubercles. Above the ambitus each plate has a single perforate and crenulate, centrally-positioned primary tubercle, arising from a small node which elevates the tubercle. The rest of the plate has a semi-regular arrangement of similar-sized tubercles with a dense, irregular array of miliary tubercles between them. Below the ambitus, tubercles are larger and the miliary tubercles become less noticeable; there are a maximum of three tubercles on each plate with two smaller tubercles adradially. Areoles are enlarged on the adambital side of the boss.

REMARKS. This is a very well known species which shows a certain amount of variability in shape (see Smith & Paul, 1985). *D. subuculus* most closely resembles *D. inferus* but differs in having a proportionally larger peristome and a dense and irregular dorsal miliary tuberculation.

Discoides inferus (Desor 1847)

Pl. 15, figs 4–6; Pl. 19, fig. 2; Fig. 35.

1847 *Discoidea infera* Desor, *in* Agassiz & Desor: 147.
1849 *Discoidea infera* Desor; Forbes: explanation to pl. 7, p. 4.
1861 *Discoidea infera* Desor; Cotteau: 37; pl. 1013, figs 1–9.
1869 *Discoidea infera* Desor; Cotteau & Triger: 380; pl. 63, figs 1–5.
1985 *Discoides infera* (Desor) Smith & Paul: text-fig. 2, E, F.

MATERIAL. Four specimens have been collected at Wilmington of which only one (E.80897) is well preserved and is described below. The other three specimens (E.82713–5) are all small individuals.

STRATIGRAPHICAL OCCURRENCE AND DISTRIBUTION. At Wilmington the specimens were collected from the basal part of the Middle Chalk, from 6 cm to 95 cm above standard datum level. All are unphosphatized and belong to the *I. labiatus* Zone, Lower Turonian.

DESCRIPTION. *SIZE AND SHAPE.* The test is circular in outline with a diameter of 11·5 mm. The base is gently rounded and the peristome slightly sunken. In profile, the test is roundedly conical with a broad flat base and a low ambitus. Test height is 70% of the test diameter and the ambitus lies at approximately 15% of the test height above the base. The tallest point on the test is central and coincides with the apical disc.

APICAL SYSTEM. The apical disc is approximately circular with a diameter 11% of the diameter of the test, and lies at its apex. As far as can be seen it resembles the apical disc of *D. subuculus* in the layout of plates. Genital plate 5 is apparently imperforate but gonopores are present in the four other genital plates.

AMBULACRA. These are relatively narrow and taper adapically. At the ambitus the ambulacral zone is 17% of the test length in width. Ambulacral pores are arranged uniserially right to the peristome and they are all P_2-type isopores with a narrow attachment rim and a narrow interporal partition. Ambulacral plating is simple adapically but adorally the plates are arranged in triads with one enlarged plate and one demi-plate in each triad. There are 52 plates per column in the ambulacra.

INTERAMBULACRA. At the ambitus, the interambulacral zones are almost $2\frac{1}{2}$ times as broad as the ambulacral zones. All interambulacra are identical, the plates broader than tall, with 18 plates per column in this specimen. Adapical plates each have a slight central node

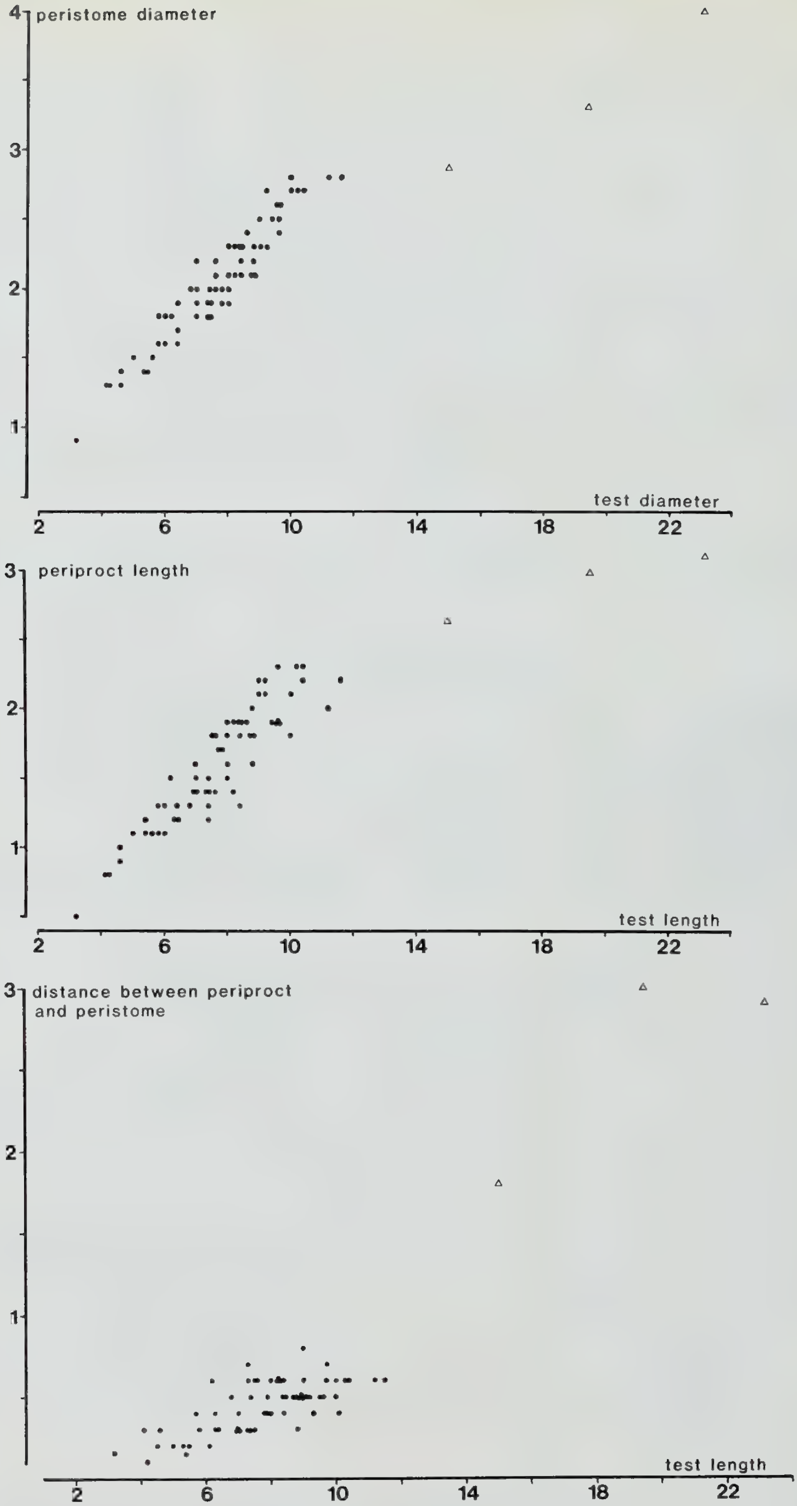


Fig. 38 Biometric data on *Discoides subuculus* (●) and *D. favrinus* (△) from Wilmington.

which supports the primary tubercle. There are two plates per column between the peristome and the periproct and plates 2a–7a and 2b–7b are separated by the periproct.

PERIPROCT. This lies on the oral surface, midway between the peristome and the ambitus. It is relatively large and biconvex in outline. Its length is 23% of the test length, which is only very slightly less than the diameter of the peristome. At its broadest, the periproct width is 67% of its length. The distance between the adoral edge of the periproct and the peristome is 7% of the test length and the distance between the adambital edge of the periproct and the ambitus 9% of the test length.

PERISTOME. The peristome is small and circular in outline with very feeble buccal slits. It has a diameter that is 24% of the test diameter, and lies slightly sunken.

TUBERCULATION. There is a clear differentiation between the tuberculation of adoral and adapical surfaces. Adapical tubercles are minute and widely scattered. There is a tiny primary tubercle to each plate situated on the central node, and a semiregular arrangement of other tubercles (Pl. 19, fig. 2). Miliary tubercles are arranged into discrete rows that radiate from the primary tubercles leaving small wedge-shaped spaces devoid of tubercles. At the ambitus tuberculation changes sharply. Adoral tubercles are considerably larger and more closely packed together. Miliary tubercles are irregularly arranged and lie scattered amongst the larger tubercles although interradially there is a wedge-shaped zone devoid of larger tubercles and with only miliary tubercles. Major tubercles are perforate, crenulate and slightly sunken. Their areoles are enlarged to the adambital side of the boss.

REMARKS. This species closely resembles *D. subuculus* but is distinguished by having a proportionally smaller peristome and by its very distinctive tuberculation, especially in the radial alignment of miliary tubercles on adapical plates. *D. minimus* Agassiz is also rather similar but never achieves the size of *D. inferus*, has a more rounded profile and an even smaller and less sunken peristome. *D. inferus* was first described in Agassiz & Desor (1847) by Desor, who separated it from *D. subuculus* on its smaller adapical tuberculation. Cotteau (1861) gave the first figures of this species, in which the distinctive arrangement of adapical tubercles was clearly shown. He pointed out that, in comparison with *D. subuculus*, in *D. inferus* adapical interambulacral nodes were less pronounced, that the periproct was proportionally larger and that all five genital plates were perforate. In the Wilmington specimen genital plate 5 is imperforate, but in other respects it is identical with Cotteau's specimen. If this difference in the number of gonopores is consistent within populations then the two forms should probably be separated as distinct species but until more specimens become available for study, I prefer to treat them as subspecific varieties.

Discoides favrinus (Desor 1842)

Pl. 16, figs 1–3; Figs 38–39

1842 *Discoidea Favrina* Desor: 62; pl. 7, figs 12–14.
1849 *Discoidea Favrina* Desor; Forbes: explanation to pl. 8, p. 6.
1858 *Discoidea Favrina* Desor; Desor: 178.
1873 *Discoidea Favrina* Desor; Wright: 210; pl. 48, fig. 1.
1914 *Discoides Favrei* (Desor) Lambert & Thiéry: 282.

MATERIAL. Two specimens of *D. favrinus* were collected at Wilmington (E.80855–6), one of which was *in situ*. The following description is based on these specimens, but a number of others from the Cenomanian Bed B of the south Devon coast were also studied for comparison.

STRATIGRAPHICAL OCCURRENCE AND DISTRIBUTION. The one specimen from Wilmington collected *in situ* comes from the top of the Grizzle, 110 cm below standard datum level. The matrix infilling the other specimen suggests that it also came from the Grizzle. Elsewhere, *D. favrinus* is moderately common in the Middle Cenomanian Bed B (*A. rhotomagense* Zone) of the south Devon coast.

DESCRIPTION. *SIZE AND SHAPE.* The two specimens are very slightly pentagonal in outline and measure 15·0 and 23·2 mm in diameter. They have a uniformly domed dorsal surface with

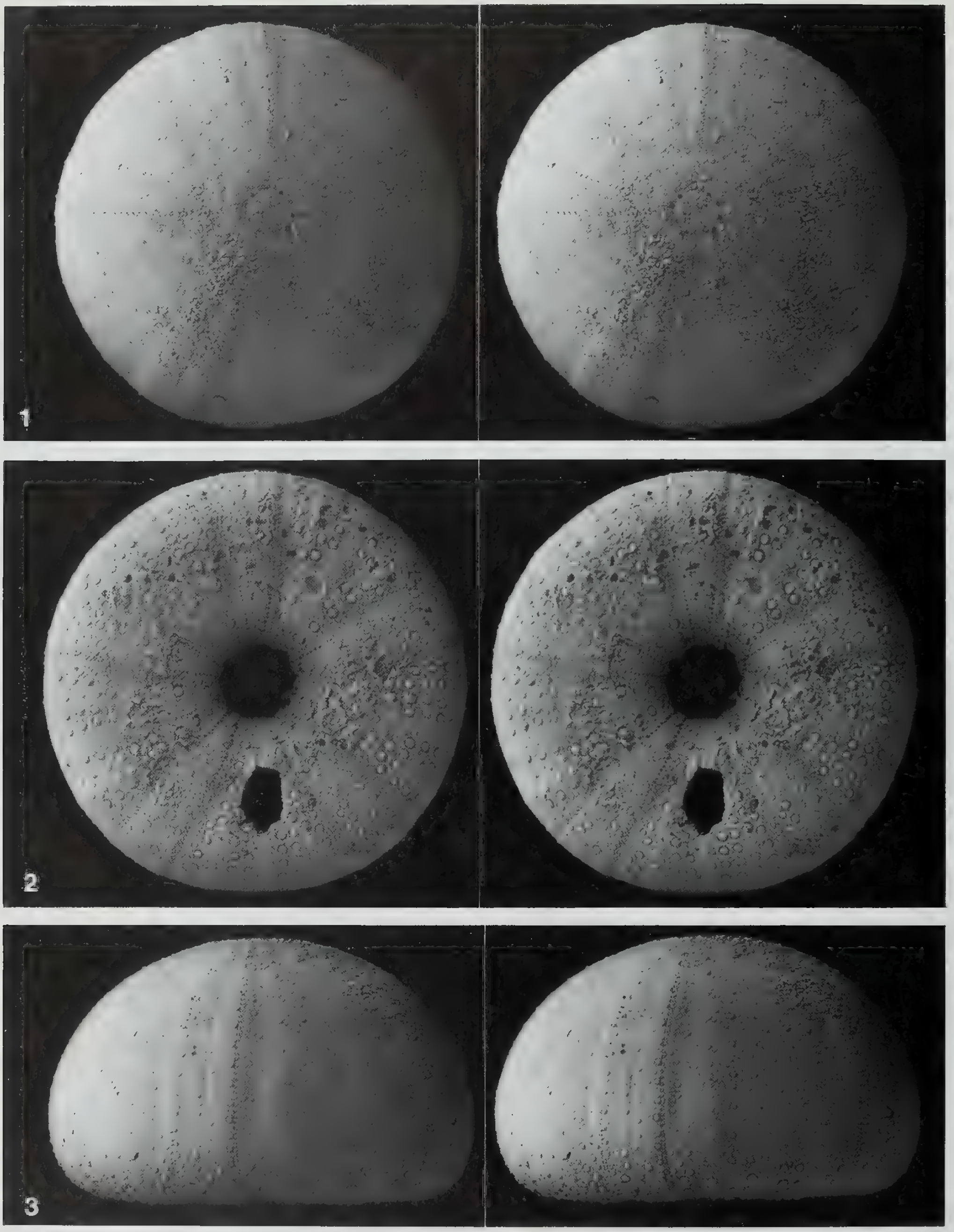


Plate 16
Discoides favrinus (Desor)
Figs 1–3 E.80855: 1, apical; 2, oral; 3, lateral. Top of the Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 2·5).

a height 59–60% of the diameter. In profile the test has a broad flat base. The tallest point on the test is central and coincides with the apical disc. The ambitus lies about 20% of the test height above the base. The oral surface is slightly convex and the peristome is moderately sunken.

APICAL SYSTEM. The apical disc is centrally positioned and is roughly circular in outline with a diameter of about 12% of the test length. There are five genital plates, four of which have gonopores. Only the posterior genital plate is imperforate (Fig. 39b). Genital plate 2 is a little larger than the rest and abuts against all the others. Hydropores perforate all five genital plates, but are best developed on genital plate 2. Ocular plates are small and triangular.

AMBULACRA. These are relatively narrow and at the ambitus measure 14–16% of the test diameter in width. Ambulacra taper slightly adapically and all five ambulacra are identical and flush. Ambulacral pores are arranged uniserially above the ambitus and in weak arcs of three subambitally. They are P_2-type isopores from apex to peristome, with a narrow attachment rim. The isopores are small and occupy about 10% of the plate width at the ambitus. In the 23·2 mm individual there are 112 isopores per ambulacral column. Ambulacral plates are elongate and low. Above the ambitus ambulacral plating is simple and all plates reach the perradial suture. A larger tubercle occurs adradially on every third plate, but all plates have a single row of small tubercles. Near the ambitus and subambitally a second, more perradial tubercle is present and alternates with the primary tubercle. From the ambitus adorally the plating becomes pseudocompound with every third plate enlarged and extending to the perradial suture. The other two plates are much shorter and occluded from the perradius. The large plate in each triad has a large tubercle; the other plates have only a few miliary tubercles. Adorally, successive triads are identical but subambitally alternate triads are large and small. Isopores are most densely packed subambitally and become more widely spaced both adapically and adorally.

INTERAMBULACRA. Interambulacral zones are about three times as broad as the ambulacral zones at the ambitus and measure 47% of the test diameter in both specimens. There are 21 plates per column in the 15 mm diameter specimen and 23 plates in the 23 mm diameter specimen. The plates are moderately tall above the ambitus and over most of this region there are six ambulacral pores opposite each interambulacral plate. There are small scattered primary tubercles on each plate, with a slightly larger central tubercle. Miliary tubercles occur over the rest of the plate but are not closely packed. Subambitally the primary tubercles become noticeably larger, more common and more closely packed with fewer miliary tubercles.

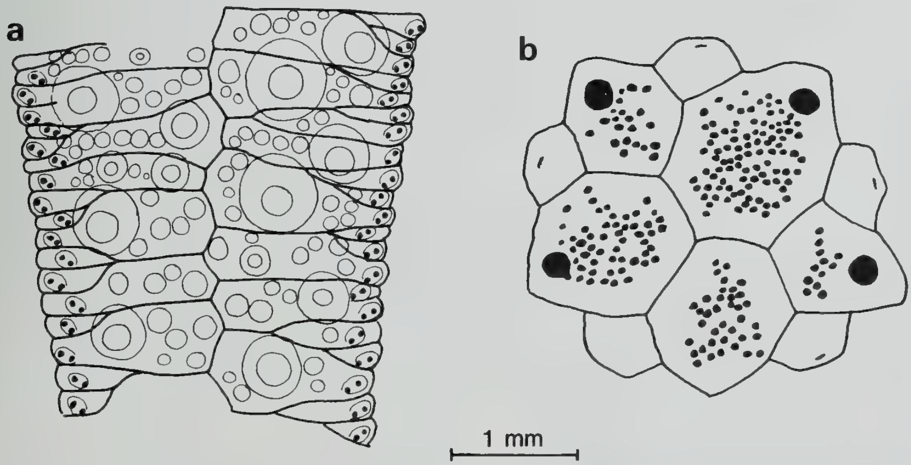


Fig. 39 Camera lucida drawings of *Discoides favrinus* (E.80855) from the Lower Cenomanian of Wilmington: a, sub-ambital ambulacral plating; b, apical disc.

There are four interambulacral plates per column between the peristome and the periproct. The periproct is bounded by four or five plates on each side.

PERIPROCT. This is lenticular in outline, being slightly pointed both adorally and adambitally; its length is 16 or 17% of the test length and its width 65–74% of its length. The periproct lies orally approximately midway between the peristome and the ambitus. The distance from the adoral edge of the periproct to the peristome is 12% of the test length and from the ambital edge of the periproct to the ambitus is 10–13% of the test length.

PERISTOME. The peristome is relatively small and circular in outline. It is situated centrally and has a diameter 17–19% of the test diameter. There are very feeble gill slits present, but they are hardly noticeable. The peristome is slightly sunken and the test curves inwards close to the peristome.

INTERNAL BUTTRESSING. Ten strong radial ridges are present adorally, lying close to the adradial sutures on interambulacral plates. These are well developed close to the peristome but disappear adambitally. The structure of the perignathic girdle is unknown.

TUBERCULATION. Dorsal tubercles are very small and scattered and the dorsal surface appears almost smooth to the naked eye. Tubercles on the oral surface are more prominent and more densely packed. They have areoles that are enlarged adambitally.

REMARKS. *D. favrinus* was first described and figured by Desor (1842) and was first recorded in Britain by Forbes (1849). It is morphologically intermediate between *Discoides subuculus* and *Camerogalerus cylindricus*. It differs from *D. subuculus* in having a proportionally smaller periproct and peristome, and a greater distance, comprising four interambulacral plates per column instead of two, separating periproct and peristome. It has six ambulacral pores opposite an ambital interambulacral plate, not four. In addition the madreporic pores extend over all five genital plates in *D. favrinus* but are confined to genital plate 2 in *D. subuculus*, and subambitally two of the three plates in each triad are occluded from the perradius whereas only one plate in every three is occluded in *D. subuculus*.

D. favrinus differs from *Camerogalerus cylindricus* in having a more convex base and a proportionally larger peristome and periproct. In *Camerogalerus* 6–8 interambulacral plates per column separate the peristome and periproct.

Family **CONULIDAE** Lambert, 1911

Genus ***CONULUS*** Leske, 1778

Conulus castanea (Brongniart 1822)

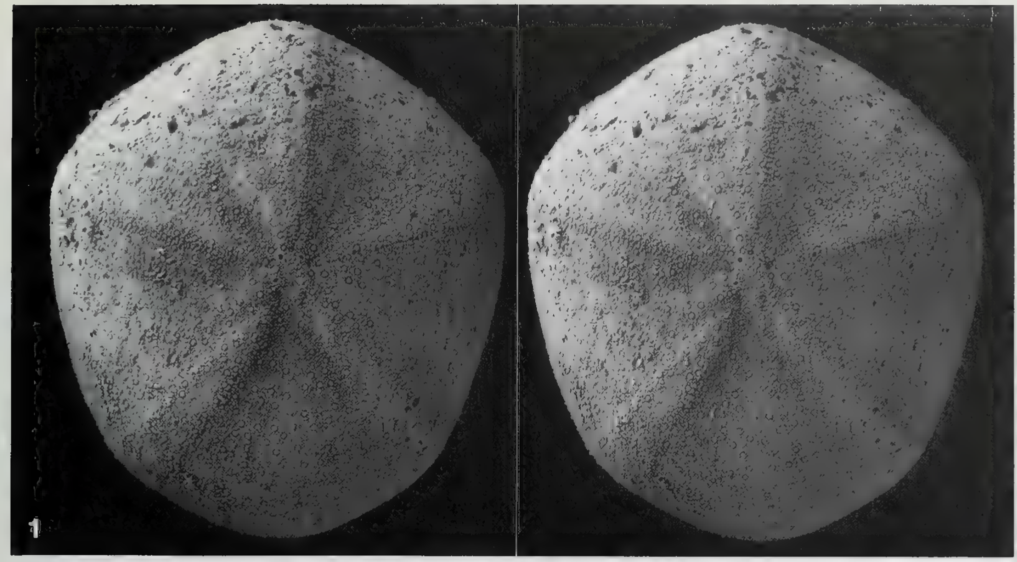
Pl. 17, figs 1–3; Pl. 18, figs 1–3; Figs 40–41.

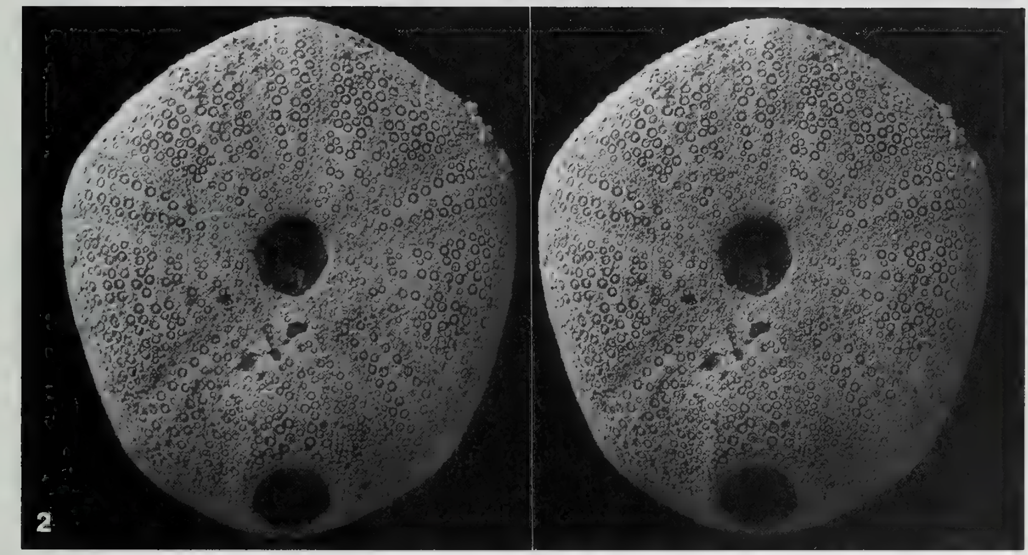
1822	*Nucleolites Castanea* Brongniart: 336, 614; pl. 9, fig. 14.
1822	*Nucleolites depressa* Brongniart: 336, 615; pl. 9, fig. 17.
1839	*Galerites Castanea* (Brongniart) Agassiz: 77; pl. 12, figs 7–9.
1839	*Galerites Rhotomagensis* Agassiz: 78.
1840*b*	*Galerites Castanea* (Brongniart); Agassiz: 7.
1840*b*	*Galerites Rhotomagensis* Agassiz: 7.
1840*b*	*Pyrina laevis* Agassiz: 7.
1850*b*	*Galerites Castanea* (Brongniart); Forbes: explanation to pl. 7.
1855	*Pyrina depressa* (des Moulins) d'Orbigny: 472; pl 981, figs 1–3.
1855	*Pyrina laevis* Agassiz; d'Orbigny: 490; pl. 987, figs 6–9.
1855	*Echinoconus Castanea* (d'Orbigny) d'Orbigny: 503; pl. 990, figs 1–5.
1855	*Echinoconus Rhotomagensis* (d'Orbigny) d'Orbigny: 509; pl. 993, figs 1–5.
1875	*Pyrina laevis* Agassiz; Wright: 238; pl. 54, fig. 1.
1875	*Echinoconus Castanea* (Brongniart); Wright: 215; pl. 51, figs 2, 3.

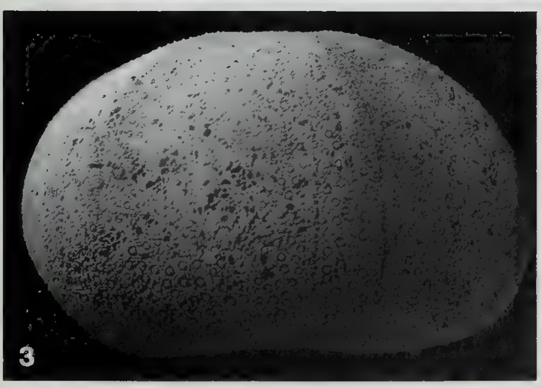
Plate 17

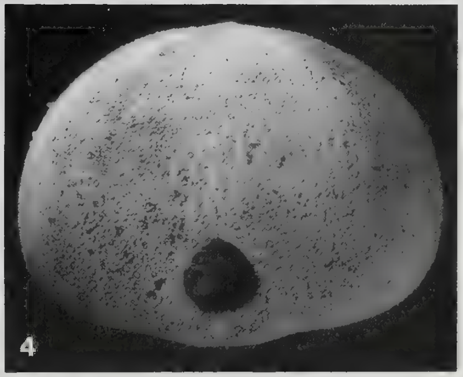
Conulus castanea castanea (Brongniart)

Figs 1–3 E.81481: 1, apical; 2, oral; 3, lateral. Upper part of the Lower Cenomanian, White Hart sand pit, Wilmington, Devon (×2·8).


1


2


3


4

1914 *Conulus castaneus* (Brongniart) Lambert & Thiéry: 284.
1935 *Conulus laevis* (d'Orbigny) Smiser: 40; pl. 4, fig. 1.
1935 *Conulus nucula* Smiser: 39; pl. 3, fig. 6 [*non* Gras].
1955 *Conulus castaneus* (Brongniart); Szörényi: 44; pl. 2, figs 5–7.

MATERIAL. Some forty specimens of *C. castanea* were collected from Wilmington of which 22 (E.80876–906) were used in the biometric analysis. Twenty of these correspond with *C. castanea, sensu stricto* and two with *C. castanea rhotomagensis.* The description is based on the specimens of *C. castanea* alone; the differences that distinguish *C. castanea rhotomagensis* are discussed on p. 112.

STRATIGRAPHICAL OCCURRENCE AND DISTRIBUTION. This species is found at two main horizons within the succession at Wilmington. It is moderately common towards the top of the Grizzle from 89 to 140 cm below standard datum. At this level the vast majority of specimens are flattish forms corresponding to *C. castanea, sensu stricto.* Phosphatized specimens are also found in the phosphatic pebble bed (Bed C), from 5 to 16 cm above standard datum. Most specimens from this horizon correspond to *C. castanea rhotomagensis.* A single specimen, too poorly preserved to be ascribed to either form, was collected from the Wilmington Limestone, 56 cm below standard datum. This species in both its forms therefore occurs throughout much of the Cenomanian, from the *M. dixoni* Zone of the Lower Cenomanian to at least the *C. guerangeri* Zone of the Upper Cenomanian.

DESCRIPTION. *SIZE AND SHAPE.* Specimens range in length from 6·7 to 29·1 mm (mean = 20·0 mm; SD = 5·3; N = 10). It has a slightly angular, egg-shaped outline tapering posteriorly, and is almost as broad as long in juveniles but becomes rather more elongate in larger individuals (test width = 88–96% of the test length; mean = 92%; SD = 2·4; N = 20). The broadest point on the test lies a little anterior of the midline and coincides with the posterior region of ambulacra II and IV in adults. The distance from the anterior of the test to the broadest point is 37–50% of the test length (mean = 45%; SD = 3·5; N = 20). The test tapers posteriorly to a rounded point. Test height is 63–76% of the test length (mean = 69%; SD = 4·4; N = 20) and the tallest point coincides more or less with the apical disc, lying 48–56% of the test length from the anterior border (mean = 53%; SD = 4·2; N = 20). In profile the test has a broad and flat or slightly concave base, a smaller flattened or slightly convex adapical region and strongly curved anterior and posterior faces.

APICAL SYSTEM. The apical disc is slightly longer than broad and is situated at the highest point on the test, about 45% of the test length from the anterior end. It is a compact tetrabasal apical disc (Fig. 41b). Genital plate 2 is slightly larger than the other genital plates and is in contact with them all. It has relatively few hydropores perforating it. Gonopores are first seen in individuals about 18 mm in length. Genital plates 1 and 4 are in contact with the posterior of genital plate 2. Ocular plates II, III and IV are small and triangular in outline and are well separated. Ocular plates I and V are a little larger and have a more rectangular outline. They meet along the posterior mid-line.

AMBULACRA. These are relatively narrow, measuring 14–19% of the test length in breadth at the ambitus (mean = 17%; SD = 1·4; N = 18). They are straight and taper adapically, where in many specimens they are weakly convex, forming feeble ridges. The ambulacra are non-petaloid and ambulacral pores are identical from apex to peristome. The pores are small partitioned isopores with a narrow attachment rim and a thin interporal partition, but adorally the interporal partition may be lost in some cases. Ambulacral pores are arranged uniserially above the ambitus but in oblique arcs of three subambitally. There are 82 ambulacral pores per column in an individual 18 mm in length, but this rises to 108 ambulacral pores in individuals 27–29 mm in length. Ambulacral plating is pseudocompound. Plates are arranged in groups of three (except at the ambitus where plating is slightly more irregular), two of which extend to the perradial suture. The third plate is small, bears no tubercle and does not reach the perradius (Fig. 41a).

INTERAMBULACRA. The interambulacral zones are about $2\frac{1}{2}$ times as broad as the ambulacra at the ambitus and in breadth are 36–42% of the test length (mean = 40%; SD = 1·7; N = 18). The plates are relatively tall and there are about five ambulacral pores

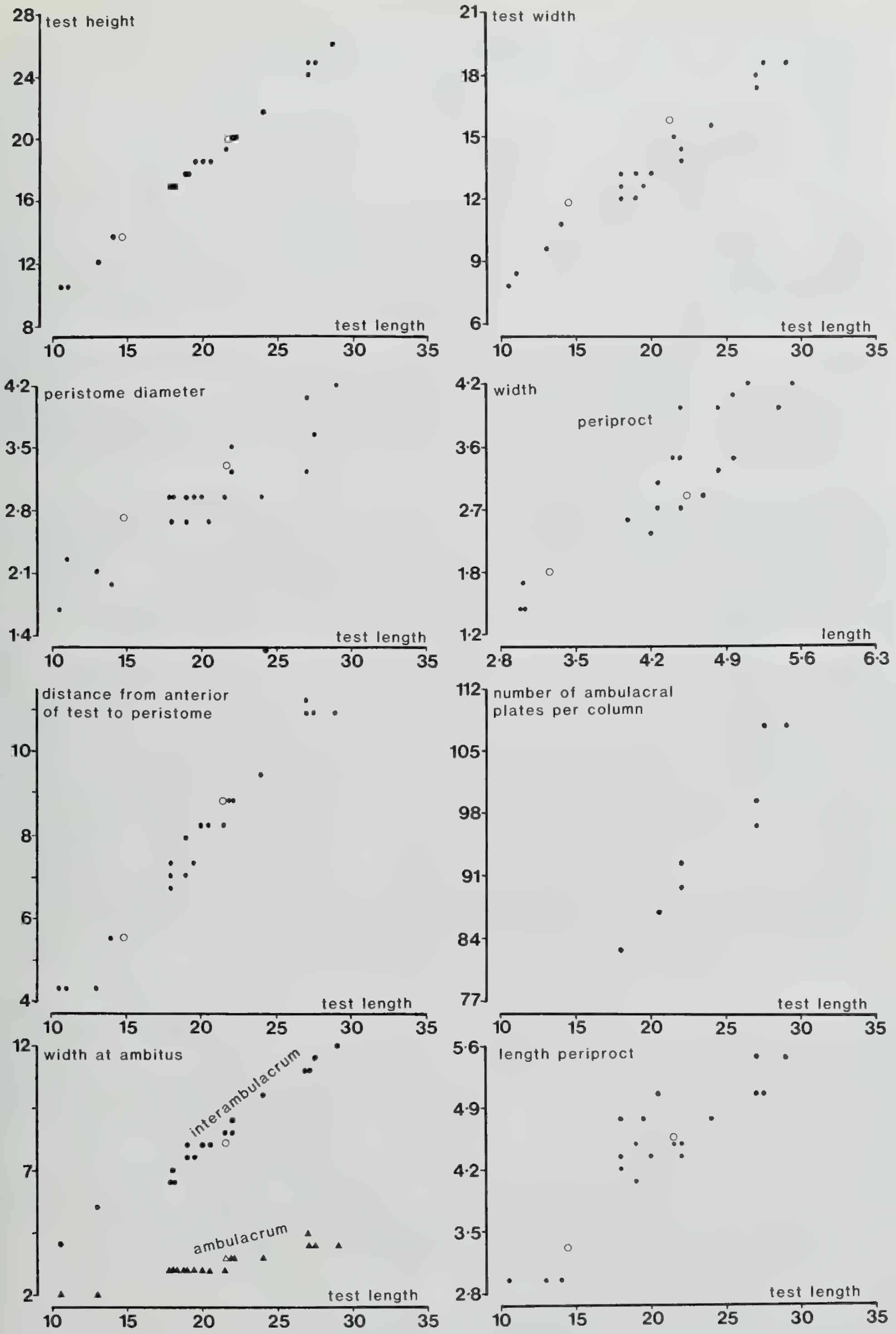


Fig. 40 Biometric data on *Conulus castanea* from Wilmington. *C. c. castanea*, ●, ▲; *C. c. rhotomagensis*, ○, △.

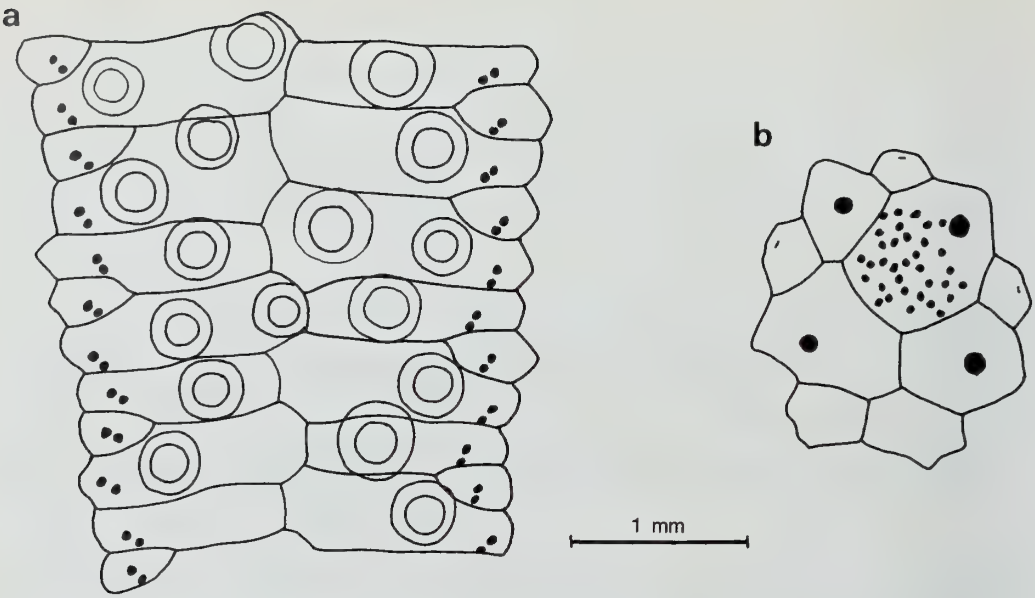


Fig. 41 Camera lucida drawings of plating in *Conulus castanea* from the Lower Cenomanian of Wilmington: a, E.80864, sub-ambital ambulacral plating; b, E.80865, apical disc, ocular III to the top.

adjacent to each plate. There are fifteen interambulacral plates per column in an individual 13 mm in length, but this increases to 22 in individuals 27–29 mm in length (Fig. 40). Plating in all interambulacra is the same. There are nine plates per column between the periproct and the peristome and the periproct lies between plates 8a, b and 10a, b.

PERIPROCT. This lies subambitally and is visible both orally and from the posterior. It is slightly longer than broad and is teardrop-shaped in outline. It is 19–28% of the test length in length (mean = 22%; SD = 2·8; N = 19) and the width is 66–87% of the length (mean = 74%; SD = 6·3; N = 19). In the smallest specimen, 10·5 mm in length, the periproct is relatively high and the distance from the base of the test to the base of the periproct is 37% of the test height. In larger individuals the periproct is situated lower and at 27–29 mm test length the distance from the base of the test to the base of the periproct is 8–9% of the test height.

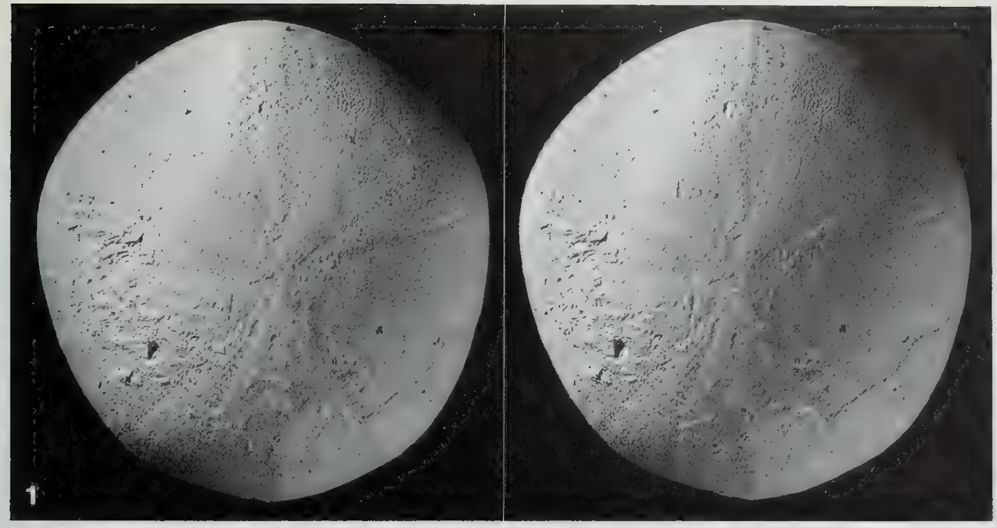
PERISTOME. The peristome is relatively small and generally rather irregular in outline. Its length is 12–20% of the test length (mean = 15%; SD = 1·8; N = 20) and its width 76–100% of the peristome length (mean = 88%; SD = 6·2; N = 20). It is very slightly sunken and the anterior edge of the peristome lies 33–41% of the test length from the anterior edge of the test (mean = 39%; SD = 1·8; N = 20). There are no buccal slits.

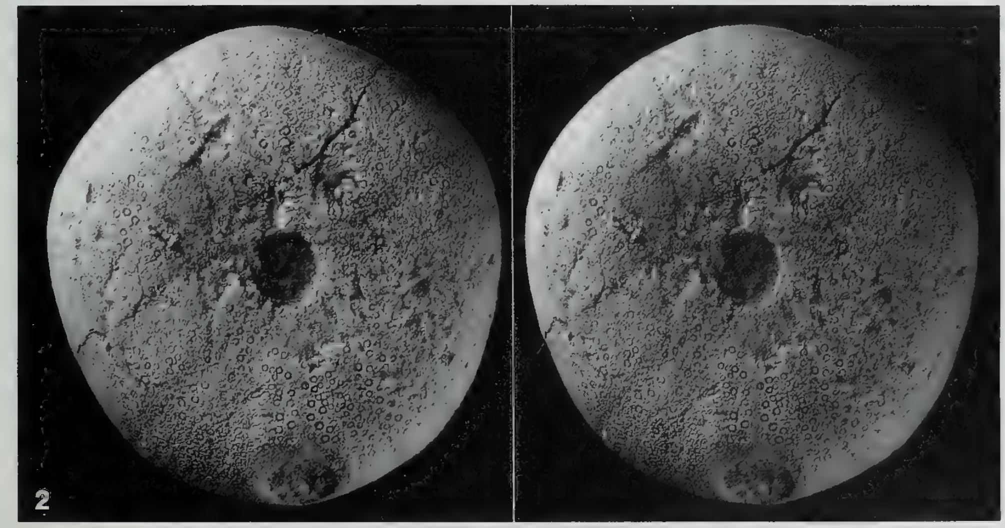
TUBERCULATION. This is relatively simple in *C. castanea*. Adoral and adapical tubercles are similar and there is no ambulacral–interambulacral differentiation. Tubercles are perforate and crenulate and are very slightly sunken. Adoral tubercles are very slightly larger and slightly more sunken than adapical tubercles. There is no apparent direction of areole enlargement to tubercles. Miliary tubercles are moderately dense on both surfaces. On the adapical surface tubercles are arranged semi-regularly. Bordering the peristome, tubercles are smaller and more densely packed and there must have been a screen of spines across the peristome in life.

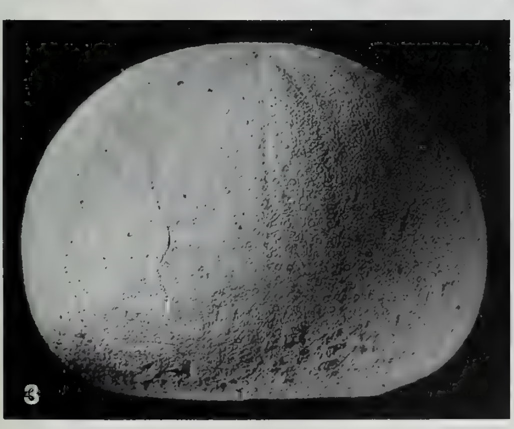
Plate 18

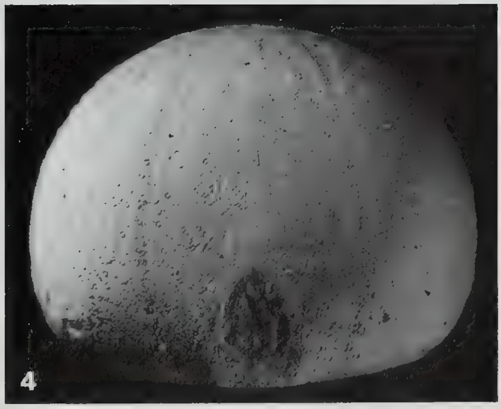
Conulus castanea rhotomagensis (Agassiz)

Figs 1–3 E.80895: 1, apical; 2, oral; 3, lateral. Upper Cenomanian (Bed C, phosphatized), White Hart sand pit, Wilmington, Devon (× 3·3).


1


2


3


4

REMARKS. There has been considerable confusion over this species in the past, particularly over the identification of juveniles. The name *Nucleolites castanea* was first used by Brongniart (1882) for an Albian species with an egg-shaped outline and a very flattened profile. In the same work, Brongniart also figured a juvenile of the same species under the name *Nucleolites depressa.* Agassiz (1839) gave an excellent figure and description of *Conulus castanea* under the name *Galerites castanea.* His specimen is a little less depressed in profile than the one figured by Brongniart (1822). Agassiz also separated *C. castanea* from a species he named *Galerites rhotomagensis* because the latter was smaller, less angular with a more or less rounded outline, and had a higher periproct and a larger peristome, but he gave no figure. This species was formally diagnosed by Agassiz one year later (Agassiz 1840*b*).

The first British record of this species was given by Forbes (1850*b*), who figured and described a tall, rather globular form of *Conulus* from the Middle Cenomanian Chloritic Marl under the name *Galerites castanea.* This is rather different in overall shape from Brongniart's species and was unequivocally placed in Agassiz' species *C. rhotomagensis* by d'Orbigny (1855) and Cotteau (*in* d'Orbigny, 1855).

A small, rather globular *Conulus* was described from the Albian by Gras (1849) under the name *Galerites nucula.* This appears to be identical in form to juvenile *C. rhotomagensis.* The name *Pyrina nucula* was later used by d'Orbigny (1855) and Smiser (1935) for small Albian and Cenomanian specimens of *C. rhotomagensis.* D'Orbigny (1855) retained *C. castanea* and *C. rhotomagensis* as separate species, stating that *C. rhotomagensis* had a taller and more rounded profile, a flatter base and the periproct situated a little higher. However, the specimen illustrated under the name *C. rhotomagensis* is absolutely identical with that figured as *C. castanea* and corresponds with Brongniart's specimen rather than Forbes' specimen.

Agassiz (1840*b*) had also briefly defined a species *Pyrina laevis*, which was later figured and described by d'Orbigny (1855) and Wright (1875). Wright's specimen came from the greensands of Warminster. This species is no more than a juvenile of the flat form of *C. castanea.*

C. castanea is rather variable in shape and two forms are present at Wilmington. One is rather flattened with an angular outline, slightly raised ambulacra and moderately large periproct, and coincides fairly precisely with Brongniart's species *C. castanea.* The other form is more globular with a more rounded outline and a slightly smaller periproct; it is identical with the specimens described by Forbes (1850*b*) and corresponds to Agassiz' species *C. rhotomagensis.* The two forms are found together in both the Grizzle and Bed C, although in different proportions. In broad structure and plate arrangement *C. rhotomagensis* is identical to *C. castanea* and the two forms differ only in test shape (compare Plates 17 and 18). The differences are not great and intermediates occur; I have therefore chosen to treat them as varieties of the same species and reduce *rhotomagensis* to a subspecies of *C. castanea.*

Conulus subrotundus (Mantell 1822)

Pl. 19, figs 3–4

1822 *Echinoconus subrotundus* Mantell: 191; pl. 17, figs 15, 18.

1875 *Echinoconus subrotundus* Mantell; Wright: 219; pl. 52, fig. 1; pl. 53, figs 2, 3 (see also for earlier references).

Plate 19

Discoides subuculus (Leske)

Fig. 1 E.81269, detail of ambital interambulacral tuberculation. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 20). See also Pl. 15, figs 1–3.

Discoides inferus (Desor)

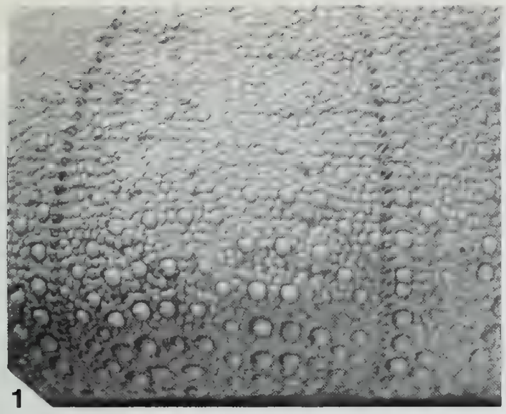
Fig. 2 E.80897: detail of ambital interambulacral tuberculation. As last (× 20). See also Pl. 15, figs 4–6.

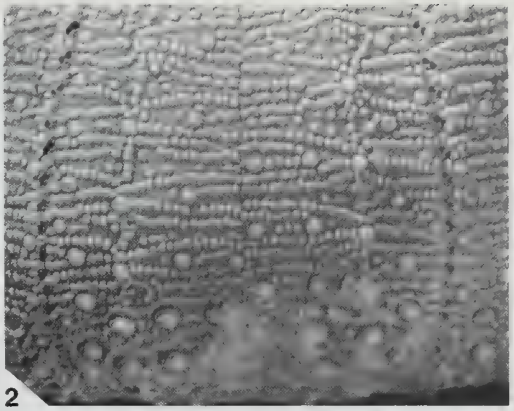
Conulus subrotundus (Mantell)

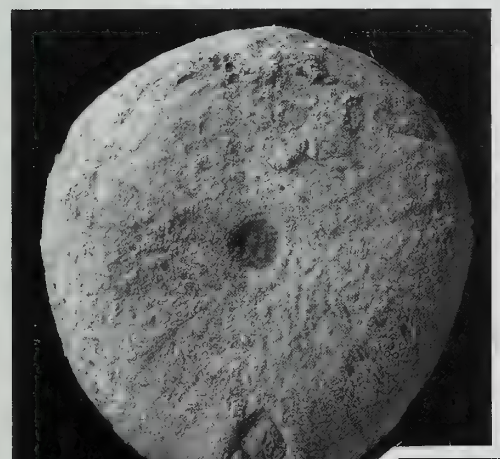
Figs 3, 4 E.80857: 3, oral; 4, lateral. As last (× 1·5).

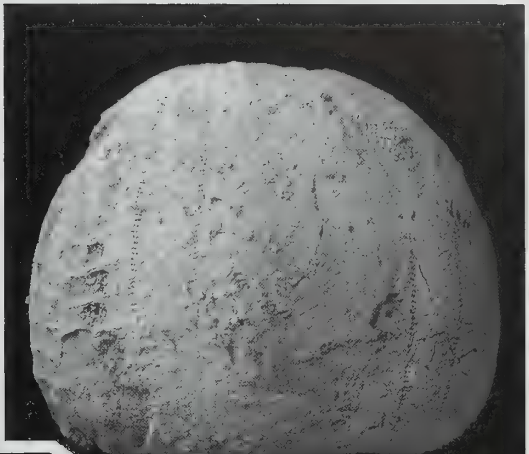
Cardiaster truncatus (Goldfuss)

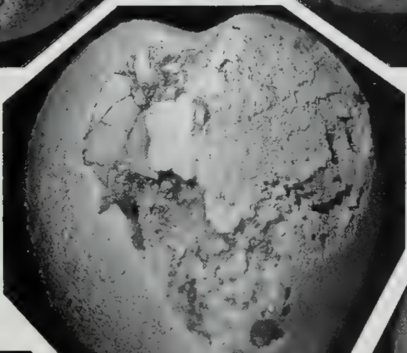
Figs 5–7 E.80195: 5, apical; 6, lateral; 7, oral. As last (× 3·3).

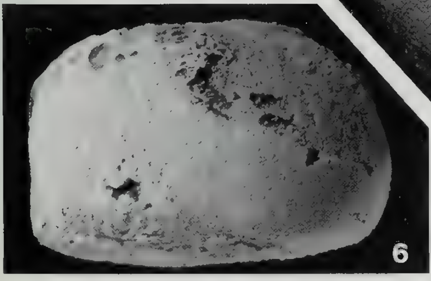

1

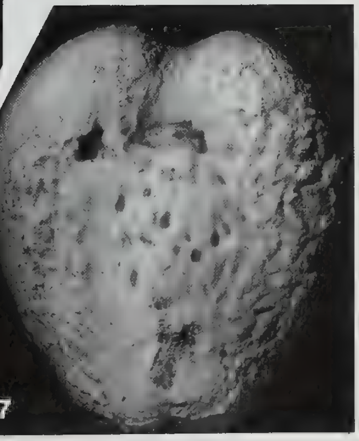

2


3


4


5


6


7

1914 *Conulus subrotundus* (Mantell) Lambert & Thiéry: 284.
1935 *Conulus subrotundus* (Mantell); Smiser: 39; pl. 3, figs 7.
1972 *Conulus subrotundus* (Mantell); Ernst: 101; fig. 16.

MATERIAL. A single specimen (E.80857) was collected *in situ* at Wilmington. It is unfortunately rather poorly preserved and only a brief description is given below.

STRATIGRAPHICAL OCCURRENCE AND DISTRIBUTION. The Wilmington specimen of *C. subrotundus* was collected in the basal glauconitic portion of the Middle Chalk, 16 cm above its base. It therefore belongs to the *I. labiatus* Zone of the Lower Turonian. Elsewhere in southern England it is a well-known species from the Turonian chalk.

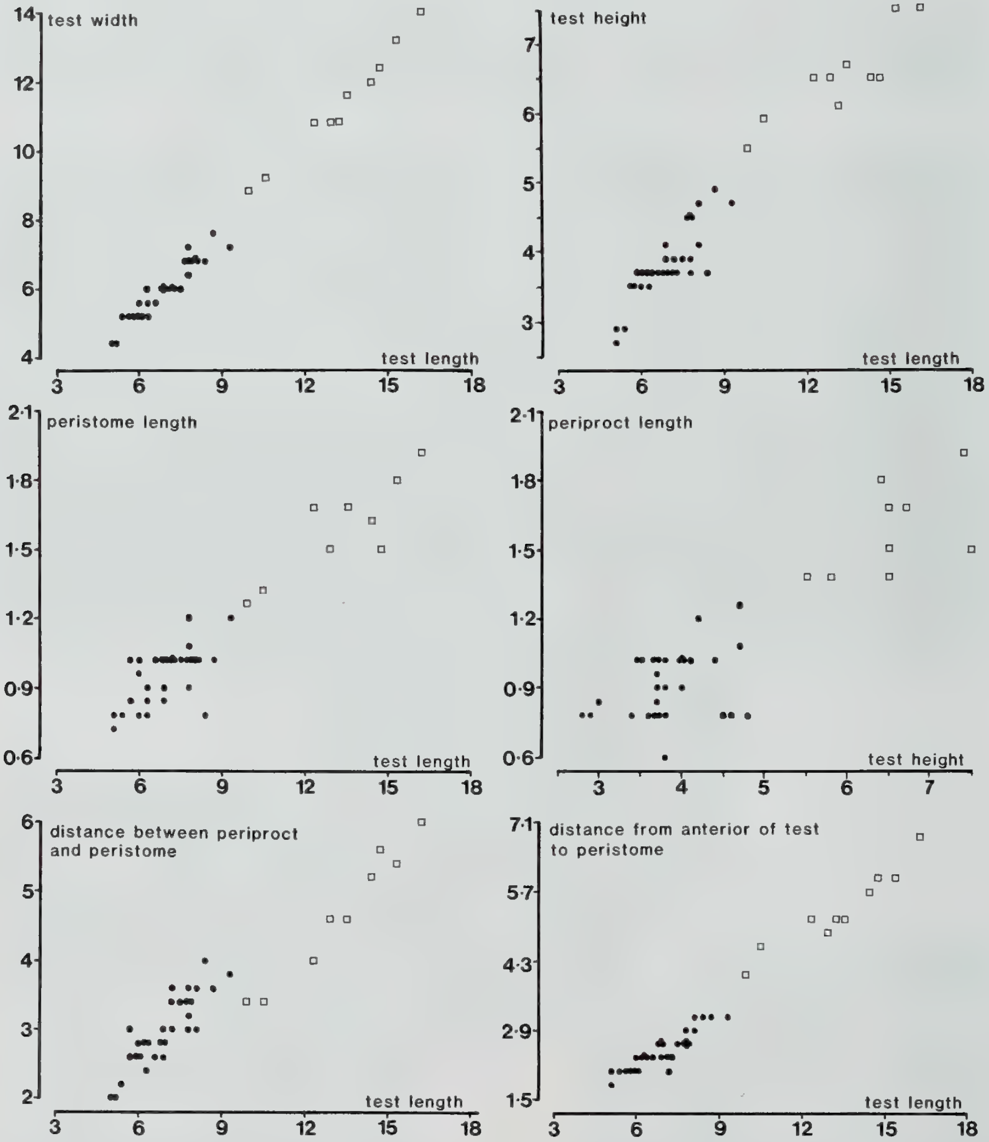


Fig. 42 Biometric data on *Echinogalerus rostratus* (●) and *E. faba* (□) from the Lower Cenomanian of Wilmington.

DESCRIPTION. *SIZE AND SHAPE*. The specimen is fairly large with a length of 48·8 mm and is egg-shaped in outline with a broad rounded anterior and a slightly tapered posterior. The test width is 44·4 mm, which is 91% of the test length, and the widest point on the test lies 44% of the test length from the anterior of the test. The test is tall with a broad flat base and a smaller flat apical region. Test height is 40·5 mm, which is 83% of the test length, and the tallest point of the test coincides with the apical disc. In profile the sides of the test are steep and gently convex and the ambitus is situated at about 28% of the test height above the base.

APICAL DISC. The apical disc is compact and tetrabasal with four large gonopores, but the plate arrangement cannot be made out. It lies very slightly anterior of the mid-point.

AMBULACRA. Ambulacral zones are narrow and non-petaloid. At the ambitus the ambulacral zone measures 12% of the test length. Ambulacral pores are uniserially arranged and are small isopores with a narrow interporal partition. Adapically they become very slightly sunken. Plating arrangement cannot be made out in this specimen but is presumably pseudocompound as in *C. castanea*.

INTERAMBULACRA. Interambulacral zones are approximately three times as broad as ambulacral zones at the ambitus. Individual plates are broader than tall and the two columns of plates in each zone taper adorally slightly. Ambitally there are five ambulacral plates opposite each interambulacral plate.

PERIPROCT. The periproct is oval in outline and opens subambitally so that it is visible both from the oral surface and when viewed from the posterior. It is 9·2 mm in length and 6·2 mm in breadth (67% of the length). The periproct length is 19% of the length of the test. Three interambulacral plates in each column form the border to the periproct.

PERISTOME. The peristome is sub-pentagonal and 5 mm in length (10% of the test length). It is slighly sunken and the anterior border of the peristome lies 41% of the test length away from the anterior of the test. The distance between the posterior edge of the peristome and the anterior edge of the periproct is 32% of the test length.

TUBERCULATION. The dorsal surface is covered in small scattered tubercles which have a circular areole and are very slightly sunken. Miliary tubercles are also sparse.

REMARKS. Although not well preserved, this specimen has such a characteristic shape that it could not be mistaken for any other species of *Conulus*. *C. subrotundus* is a well-known species first described by Mantell (1822) and later by d'Orbigny (1855) and Wright (1875), amongst others.

Family **GALERITIDAE** Gray, 1825

Genus ***ECHINOGALERUS*** König, 1825

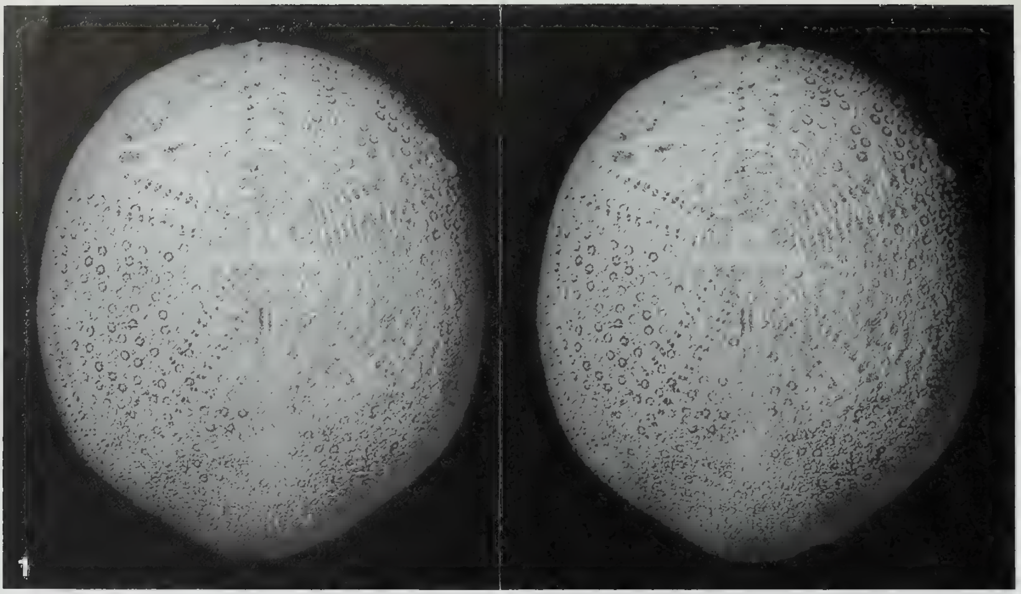
Echinogalerus faba (Desor 1842)

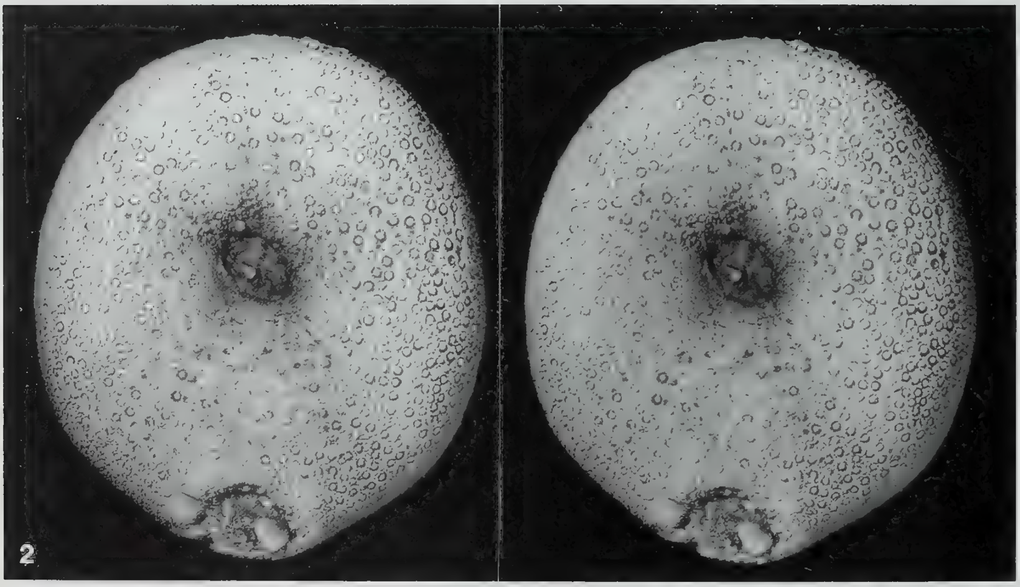
Pl. 20, figs 1–4; Pl. 21, figs 1–4; Figs 42–44

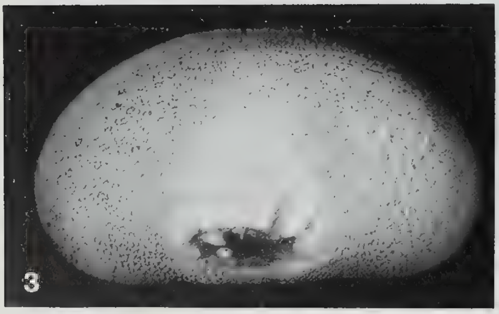
1840*b* *Caratomus Faba* Agassiz: 7 [*nomen nudum*].
1842 *Caratomus Faba* Agassiz; Desor: 37; pl. 5, figs 8–10.
1847 *Caratomus Faba* Agassiz: Agassiz & Desor: 93.
1847 *Caratomus trigonopygus* Agassiz, *in* Agassiz & Desor: 93.
1855 *Caratomus trigonopygus* Desor; d'Orbigny: 365; pl. 939.
1855 *Caratomus faba* Agassiz; d'Orbigny: 366; pl. 940.
1921 *Echinogalerus faba* (Agassiz) Lambert & Thiéry: 332.
1921 *Echinogalerus trigonopygus* (Desor) Lambert & Thiéry: 332.

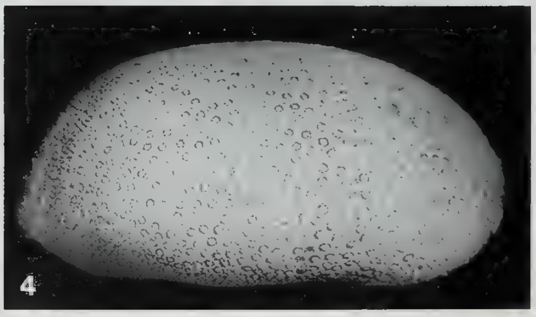
MATERIAL. Ten specimens from Wilmington (E.80898–907) were used in the biometric analysis, and form the basis for the following description. Eight were collected *in situ* and about 40 specimens were collected loose in the quarry.

STRATIGRAPHICAL OCCURRENCE AND DISTRIBUTION. This species is found only in the basal part of the succession at Wilmington, from 900 to 1027 cm below standard datum. It was first recorded in Britain by Jukes Browne & Hill (1903).


1


2


3


4

Description. *SIZE AND SHAPE.* Tests range in length from 10·0 to 16·3 mm (mean = 13·3 mm; SD = 2·0; N = 10). In outline the test is ovoid with a width 82–89% of the test length (mean = 85%; SD = 2·4; N = 10). The broadest part of the test lies 44–55% of the test length from the anterior (mean = 52%; SD = 3·4; N = 10). The anterior is uniformly rounded but the posterior of the test is drawn out to a rounded point. Test height is 44–54% of the test length (mean = 49%; SD = 3·9; N = 10), and the tallest point on the test lies at about mid-length. In profile the aboral surface is lightly convex and slopes posteriorly. The anterior is strongly curved and the ambitus lies slightly below mid-height. The oral surface is not flat, but moderately sunken around the peristome. The ambulacral zones are also slightly sunken adorally, giving the oral surface a rather undulose appearance.

APICAL DISC. The apical disc is tetrabasal and roughly circular in outline (Fig. 44a). Its length is 10–12% of the test length (mean = 11%; SD = 0·05; N = 5) and it lies at 37–42% of the test length from the anterior (mean = 39%; SD = 2·1; N = 6). Genital plate 2 is in contact with the other three genital plates. Genital plates 1 and 4 are not separated by genital plate 2. Ocular plates II, III and IV are small and triangular and are separated from one another. Ocular plates I and V are larger, more quadrate and are in contact along the midline.

AMBULACRA. Ambulacral zones are narrow and parallel-sided, tapering only in the very adapical zone. At the ambitus the width of an ambulacrum is 10–12% of the test length (mean = 11%; SD = 1·1; N = 5). The ambulacra are subpetaloid adapically. Ambulacral pores in this region are partitioned isopores, 3 mm in breadth in a 13·5 mm specimen. They have large circular pores, a narrow interporal partition, no visible attachment rim and are non-conjugate. These larger partitioned isopores extend from the apex to about $\frac{2}{3}$ of the distance to the ambitus. Adambitally the isopores become rapidly smaller and more oblique and become difficult to locate. Adorally, ambulacral pores remain relatively small and less regularly aligned, but do not become organized into phyllodes. Ambulacral plating is simple

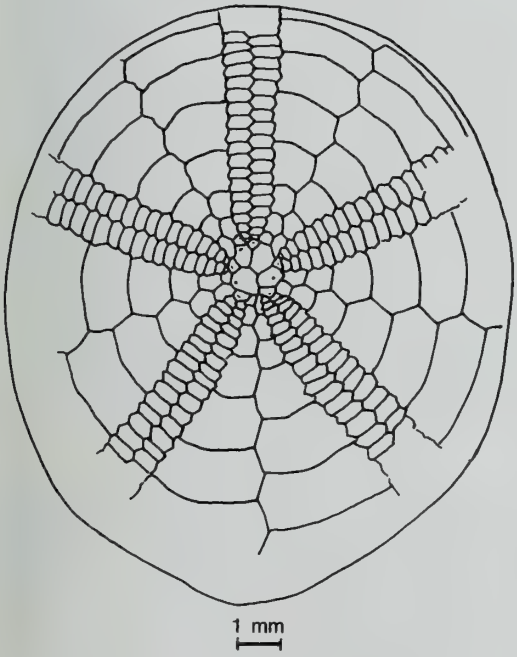
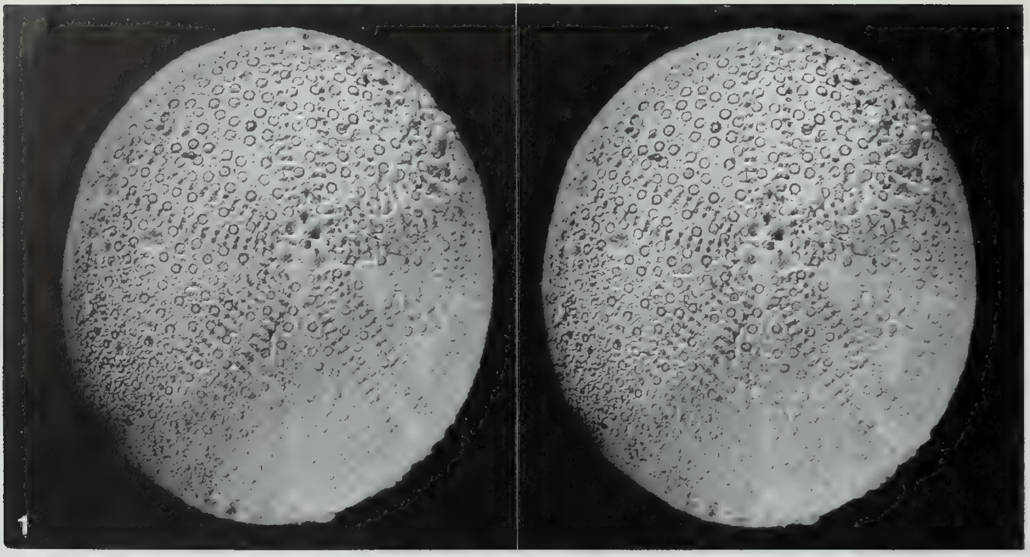
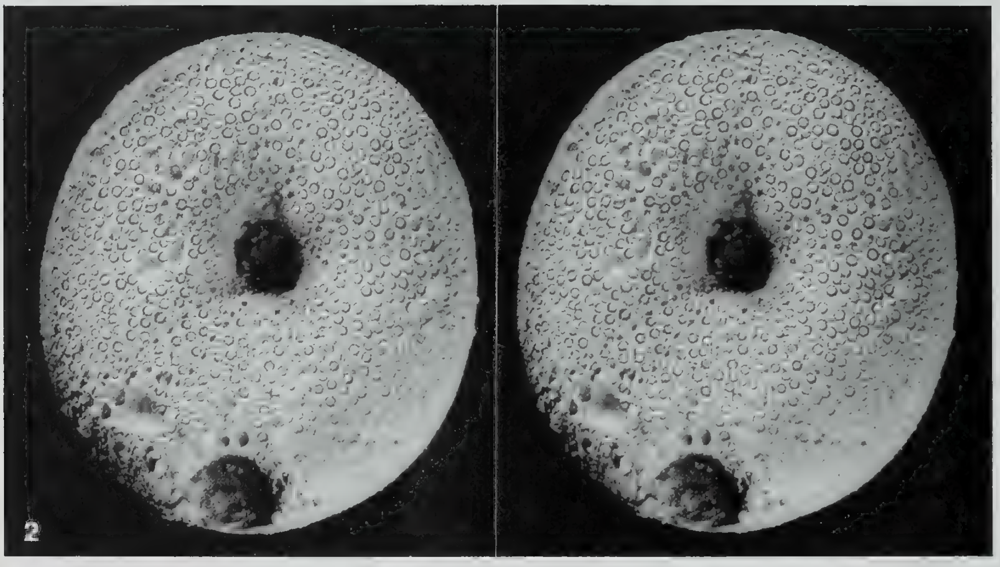
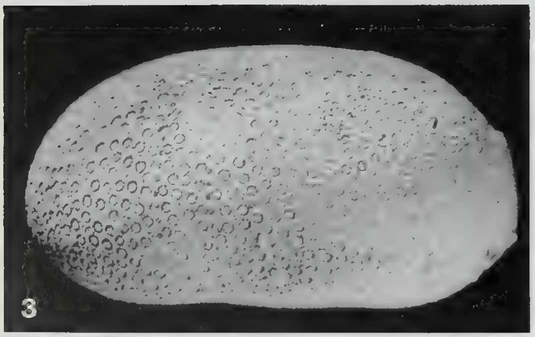


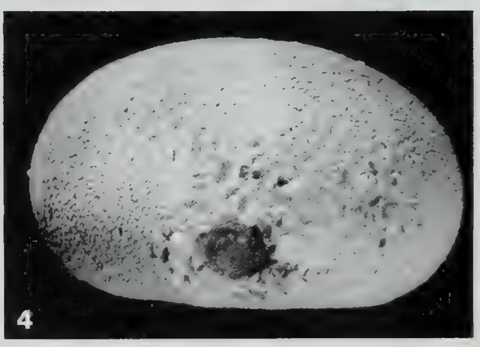
Fig. 43 Camera lucida drawing of adapical plating in *Echinogalerus faba* (E.80898) from the Lower Cenomanian of Wilmington.

Plate 20
Echinogalerus faba (Desor)
Figs 1–4 E.80898: 1, apical; 2, oral; 3, posterior; 4, lateral, anterior to right. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 5·5).


1


2


3


4

throughout and all plates are equal in size and reach the perradius. There are 38–42 ambulacral plates per column in individuals 12–13·5 mm in length.

INTERAMBULACRA. Interambulacral zones are broad and taper rapidly adapically and adorally. At the ambitus interambulacrum 2 is 31–39% of the test length in width (mean = 34%; SD = 2·8; N = 5), which is about three times the width of the ambulacral zone. Plating in all five interambulacra is identical (Fig. 43). There are five or six plates per column between the peristome and the periproct. In E.80898 the periproct lies between plates 5b, 6a and 7b, 8a.

PERIPROCT. This is subambital and triangular in outline (Pl. 20, fig. 2). Its length is 9–15% of the test length (mean = 12%; SD = 1·8; N = 9) and its breadth 1·3–2·1 times its length (mean = 1·6; SD = 0·2; N = 9). It is clearly visible from the oral surface and can also be seen, though less clearly, in posterior view. The periproct lies right at the posterior end of the oral surface and the distance separating the periproct and peristome is 33–38% of the test length (mean = 35%; SD = 1·8; N = 9).

PERISTOME. This is obliquely ovoid in outline with the long axis running from left anterior to right posterior, although it is more nearly circular in small individuals. Peristome length in the anterior–posterior axis is 10–14% of the test length (mean = 12%; SD = 1·1; N = 9) and the width is 94–106% of the length (mean = 101%; SD = 5·6; N = 9). The peristome is moderately deeply sunken and lacks buccal slits. The anterior edge of the peristome lies 37–44% of the test length from the anterior of the test (mean = 40%; SD = 2·1; N = 10).

TUBERCULATION. Tubercles are small, uniformly-sized and slightly sunken. Aboral tubercles are 0·3 mm in diameter and have a slight areole enlargement towards the mid-posterior. These tubercles are perforate and weakly crenulate. In between the larger tubercles are densely-packed miliary tubercles two or three abreast. On the oral surface, tubercles are more closely packed together and there is only a single circle of miliary tubercles separating adjacent tubercles. Areoles are enlarged slightly in a lateroposterior direction. There are no areas devoid of tubercles. Slightly smaller tubercles occur adjacent to the peristome and in life a grille of spines must have covered the peristome.

REMARKS. The first use of this name appears in Agassiz (1840*b*), but, with no accompanying diagnosis or figure, this is a *nomen nudum.* Later Desor (1842) gave a full description and an excellent figure which established the species. A second Cenomanian species *E. trigonopygus* was briefly diagnosed in Agassiz & Desor (1847). This they distinguished as being slightly rostrate posteriorly and with a triangular periproct, and later d'Orbigny (1855) gave a full description and figures of it. As d'Orbigny pointed out, the triangular shape of the periproct is a common character for all species of *Echinogalerus* and does not help distinguish the two species. He therefore based the distinction on the character that *E. faba* has a rounded posterior while *E. trigonopygus* is lightly rostrate. In the Wilmington population the rostrate posterior is variably developed; some individuals have a rounded posterior while others have a feeble posterior rostrum. The two species figured by d'Orbigny (1855) both fall within the range of variation found in the Wilmington population and *E. trigonopygus* is therefore treated here as a junior synonym of *E. faba.*

Juveniles of *E. faba* are extremely difficult to distinguish from stratigraphically low forms of *E. rostratus* and indeed some of the specimens from the base of the section listed here as *E. rostratus* may actually be juvenile *E. faba.* Adult *E. rostratus* never grow larger than 9 mm or so in length, have open gonopores by about 7 mm, have a convex base and an unsunken peristome and have a relatively large distance separating the peristome and periproct (Fig. 42, p. 114). *E. faba*, in contrast, grows to about twice that size and develops gonopores at about 12–13 mm test length. It has a well-sunken peristome and a relatively short distance separates the peristome and periproct.

Plate 21

Echinogalerus faba (Desor), juvenile

Figs 1–4 E.80899: 1, apical; 2, oral; 3, lateral, anterior to left; 4, posterior. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 5·5).

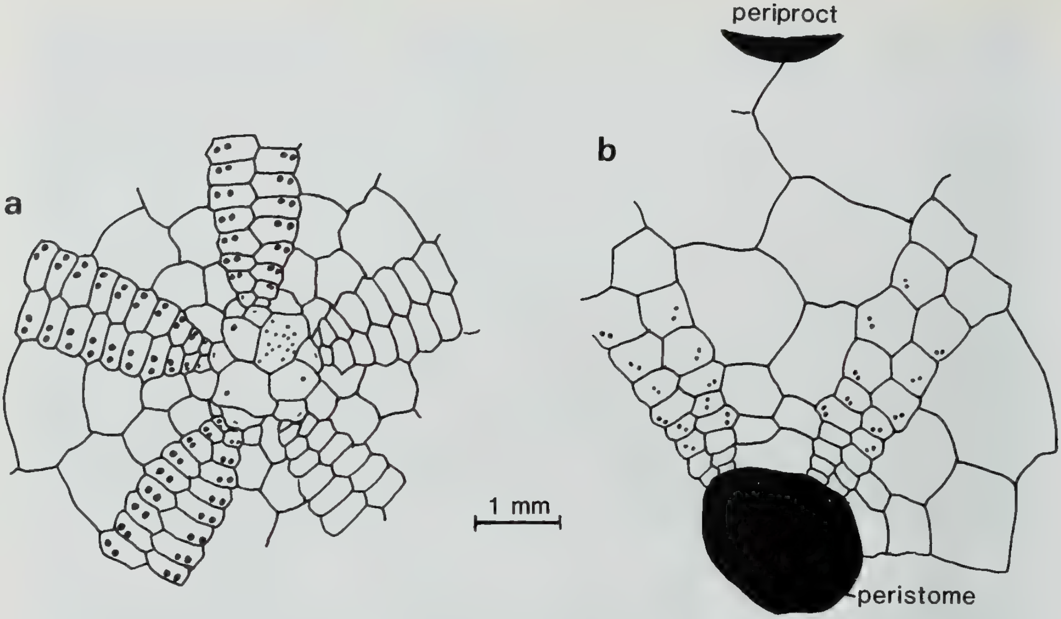


Fig. 44 Camera lucida drawings of plating in *Echinogalerus faba* (E.80898) from the Lower Cenomanian of Wilmington: a, apical disc; b, oral area between peristome and periproct.

Echinogalerus rostratus (Desor 1842)

Pl. 22, figs 1–4; Pl. 23, figs 1–4; Pl. 24, figs 6, 7; Figs 42, 45

1840*b* *Caratomus rostratus* Agassiz: 7 [*nomen nudum*].
1842 *Caratomus rostratus* Agassiz; Desor: 38; pl. 5, figs 1–4.
1855 *Caratomus rostratus* Agassiz; d'Orbigny: 367; pl. 941, figs 1–5.
1855 *Caratomus orbicularis* d'Orbigny: 369; pl. 941, figs 6–10 [*non* Agassiz].
1875 *Caratomus rostratus* Agassiz; Wright: 255; pl. 57, fig. 2.
1921 *Echinogalerus* (*Rostrogalerus*) *rostratus* (Agassiz) Lambert & Thiéry: 332.

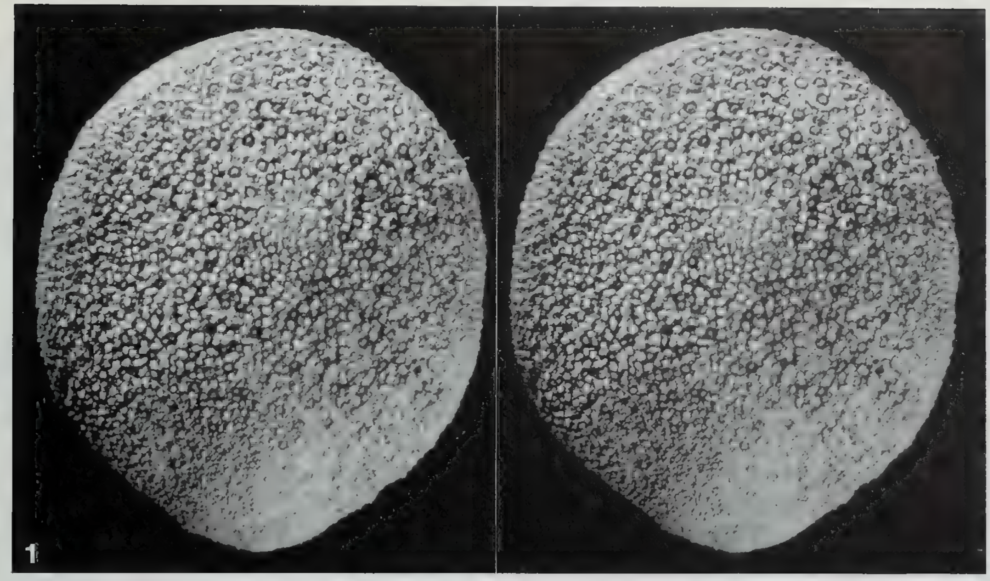
MATERIAL. This species is moderately common at Wilmington and much material both loose and *in situ* was collected. Thirty of the best preserved specimens (E.80908–37) were analysed biometrically and form the basis of the following description. All stratigraphically located material was also analysed biometrically for evolutionary changes.

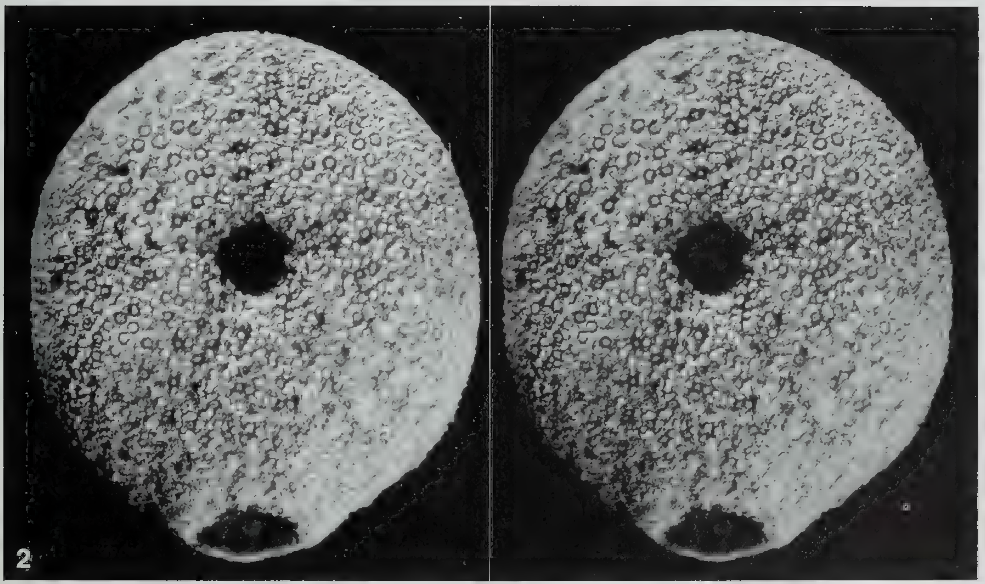
STRATIGRAPHICAL OCCURRENCE AND DISTRIBUTION. The species occurs through much of the succession at Wilmington, from 1020 cm below standard datum up to the datum level. It is most common in the Wilmington Sands from 400 to 600 cm below standard datum (Fig. 7, pp. 18–19). Two specimens have been collected from the top of the Wilmington Limestone; it thus ranges from the Lower to Middle Cenomanian. It also occurs in the Cenomanian greensands of the Warminster district.

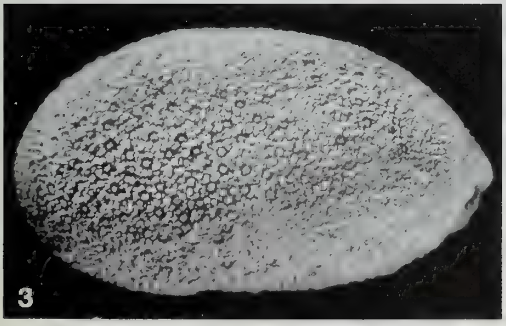
DESCRIPTION. *SIZE AND SHAPE.* This is a small species, with a test size ranging from 5·0 to 9·4 mm in length (mean = 7·0 mm; SD = 1·1; N = 30). The maximum width of the test is 78–93% of the test length (mean = 86%; SD = 4·3; N = 30) and the widest point on the test

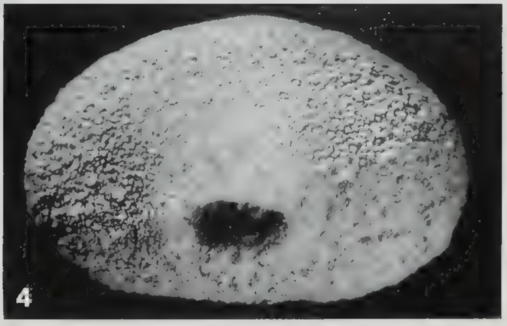
---

Plate 22
Echinogalerus rostratus (Desor)
Figs 1–4 E.80910, stratigraphically high, rostrate form: 1, apical; 2, oral; 3, lateral, anterior to left; 4, posterior. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 8·5).


1


2


3


4

lies 45–61% of the test length from the anterior (mean = 52%; SD = 3·9; N = 30). The test is ovoid in outline, usually tapering posteriorly to a rounded point which is variably developed and in some specimens absent entirely. The height of the test is 45–61% of the test length (mean = 56%; SD = 4·2; N = 30), the tallest point lying at 45–66% of the test length from the anterior (mean = 56%; SD = 5·0%; N = 29). In profile the lower surface is more or less flat while the upper surface is lightly vaulted and slopes slightly towards the anterior. The anterior is roundedly convex but the posterior comes to a slight point at the top of the periproct and is truncated, and slightly undercut. The ambitus lies slightly below mid-height.

APICAL DISC. This is relatively large and lies slightly anterior of mid-length. In a specimen approximately 8 mm in length the apical disc is 1·3 mm long and 1·0 mm broad. It is tetrabasal with genital plates 2 and 3 elongated parallel to the length of the test and genital plates 1 and 4 elongated at right angles to it. Genital plate 2 is in contact with the other three genital plates and genital plates 1 and 4 meet posterior to genital plate 2 (Fig. 45). Small gonopores are present at this size. Ocular plates II, III and IV are small, triangular and widely separated. Ocular plates I and V are more rectangular and abut one another.

AMBULACRA. The ambulacra are relatively narrow and uniform in width over most of their length. Adapically the ambulacra taper rapidly. At the ambitus the width of the ambulacra is 16–18% of the test length. Ambulacral pores are minute isopores that are difficult to find. Those adapically are slightly larger than ambital or adoral isopores but are non-petaloid. There is no concentration of isopores towards the peristome. Ambulacral plates are all simple and are almost as tall as broad. In an individual almost 9 mm in length there are 20 ambulacral plates per column.

INTERAMBULACRA. At the ambitus interambulacral zones are slightly less than twice as broad as ambulacral zones and are 26–32% of the test length in breadth. Adapical plates are roughly square but at the ambitus the plates are much broader than they are tall. Details of adoral plating are not known but five interambulacral plates per column lie between the periproct and peristome. The periproct is bordered by two or three interambulacral plates on either side.

PERIPROCT. Both the shape and the position of the periproct are rather variable. It varies from being roughly circular in outline to broad and triangular, with one point of the triangle pointing adorally. The length of the periproct ranges from 7 to 17% of the test length (mean = 13%; SD = 2·2; N = 30) and its width is between 1 and 2 times its length (mean = 1·3; SD = 0·2; N = 30). The periproct opens on the posterior face, generally subambitally. In a few specimens, particularly from low in the stratigraphical section, the periproct faces posteriorly and is not visible from the oral surface. These are non-rostrate forms. In most specimens the periproct faces slightly adorally and can be seen from the oral surface; in some

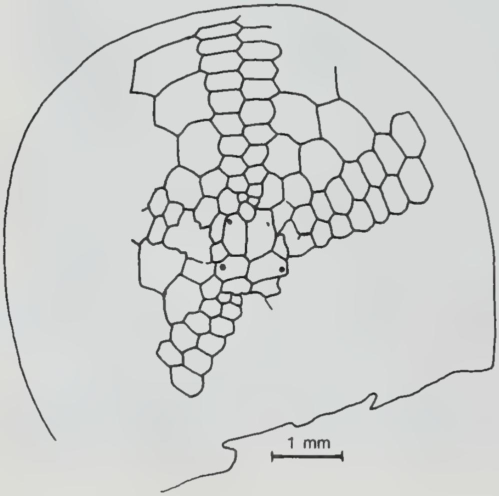
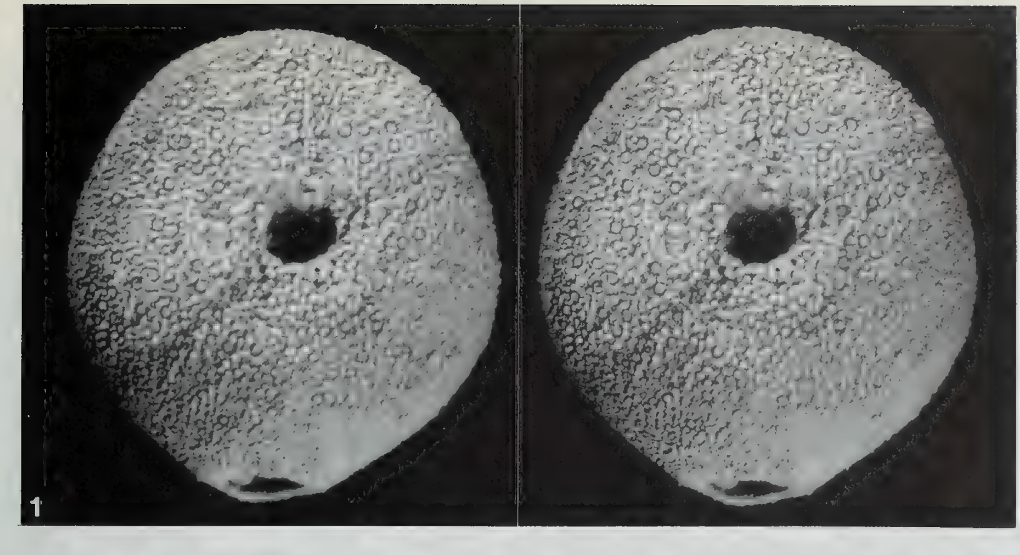
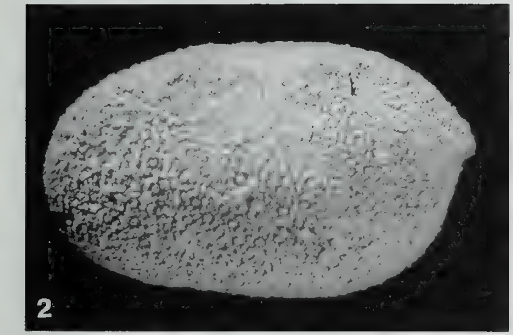
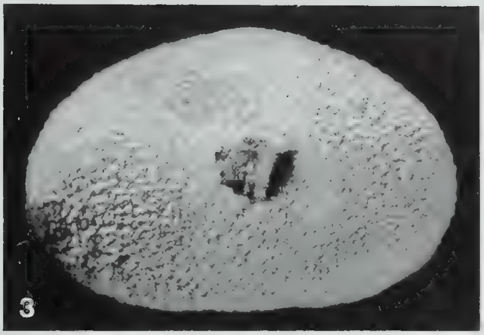


Fig. 45 Camera lucida drawing of apical plating of *Echinogalerus rostratus* (E.80937) from the Lower Cenomanian of Wilmington.







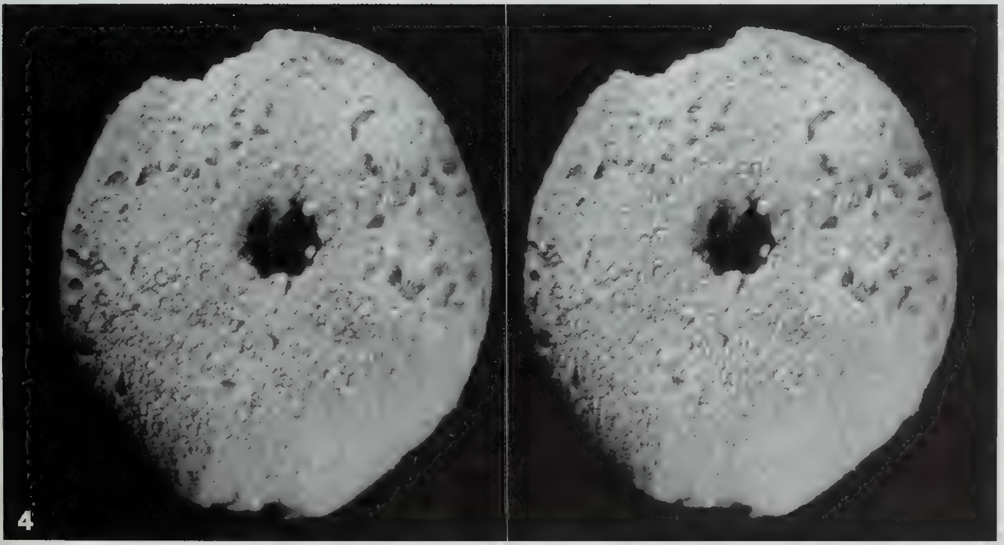
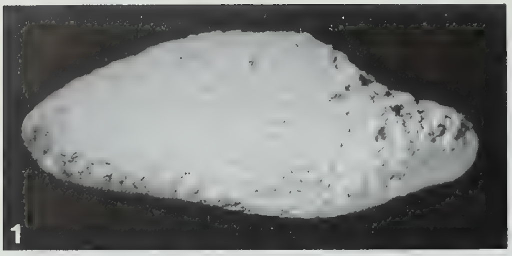


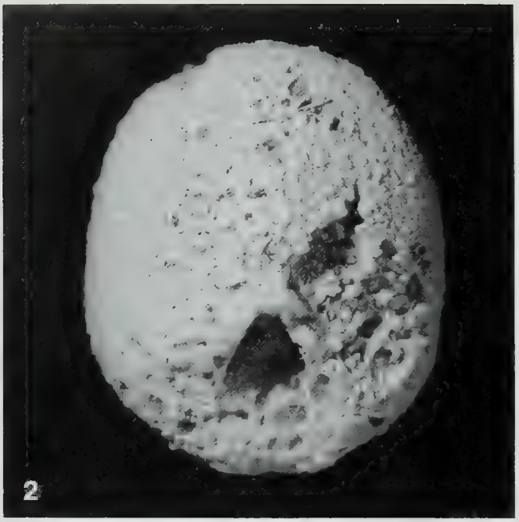
Plate 23

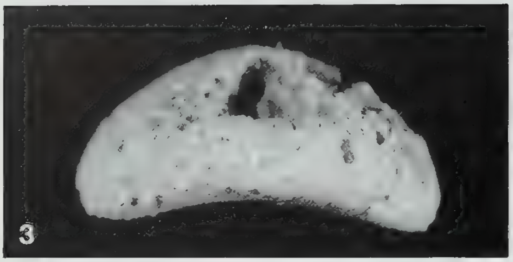
Echinogalerus rostratus (Desor)

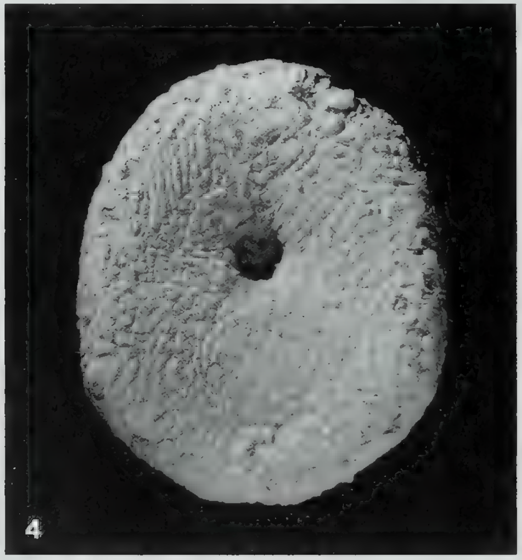
Figs 1–3 E.80908, weakly rostrate form: 1, oral; 2, lateral, anterior to left; 3, posterior. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 10).

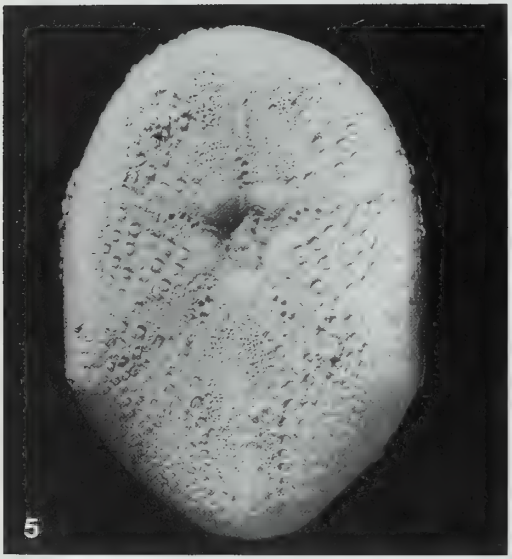
Fig. 4 E.80942, non-rostrate, stratigraphically low form: oral. As last (× 11). See also Pl. 24, figs 6–7.

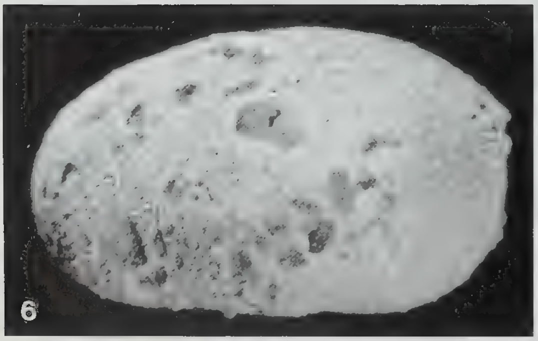

1

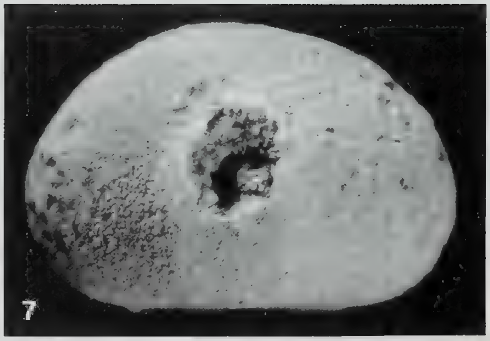

2


3


4


5


6


7

highly rostrate specimens it is almost oral in position. The distance between the periproct and the peristome is 36–50% of the test length (mean = 42%; SD = 3·5; N = 30). The base of the test to the base of the periproct measures 13–40% of the test height (mean = 31%; SD = 7·4; N = 30).

PERISTOME. The peristome is irregularly circular in outline with a length 10–17% of the test length (mean = 14%; SD = 1·6; N = 30). Its width is approximately the same as its length. The anterior edge of the peristome lies at 28–42% of the test length from the anterior of the test (mean = 36%; SD = 2·7; N = 30). The peristome may be very slightly sunken, particularly in stratigraphically low forms, but is more usually flush and in some stratigraphically high forms the oral surface becomes noticeably convex.

TUBERCULATION. This is fairly uniform over the whole test. The apical surface appears highly granular because of the dense development of elevated miliary tubercles which are almost as large as the primary tubercles. On the oral surface miliary tubercles are smaller, less densely packed and arranged as rings around the primary tubercles. These primary tubercles are a little larger than those on the apical surface, are slightly sunken and have a very slight areole enlargement on the posterior side of the boss.

REMARKS. Although the name *Caratomus rostratus* was first used by Agassiz (1840*b*) he gave no diagnosis or figure and the name did not become valid until Desor (1842) described and figured the species. It is a well-known species and was recognized in Britain by Wright (1875). D'Orbigny (1855) described a small, non-rostrate specimen under the name *Caratomus orbicularis*, but this differs from Agassiz' type specimen which is relatively large and subglobular. D'Orbigny's *C. orbicularis* lies within the range of variation of *rostratus* seen in the collection from Wilmington.

Order **CASSIDULOIDA** Claus, 1880

Family **NUCLEOLITIDAE** Agassiz & Desor, 1847

Genus ***CATOPYGUS*** Agassiz, 1836

Catopygus columbarius (Lamarck 1816)

Pl. 25, figs 1–4; Pl. 26, figs 1–4; Figs 46–49.

1811 *Echinites pyriformis* Parkinson: pl. 3, fig. 6 [*non* Leske, 1778].
1816 *Nucleolites columbaria* Lamarck: 37.
1829 *Nucleolites carinatus* Goldfuss: 142; pl. 43, fig. 11.
1847 *Catopygus columbarius* (Lamarck) d'Archiac: 296–7; pl. 13, figs 3, 3a–c.
1875 *Catopygus columbarius* (Lamarck); Wright: 241; pl. 55, fig. 2 (see also for earlier references).
1921 *Catopygus columbaris* (Lamarck); Lambert & Thiéry: 353.
1962 *Catopygus carinatus* (Goldfuss) Kier: 72; pl. 10, figs 5–8.

MATERIAL. Forty specimens (E.80648–87) were selected from the large collection of individuals collected loose at Wilmington for a biometric analysis. A further 166 specimens were accurately located within the stratigraphical succession, of which 120 (E.80688–854) were also analysed biometrically for any morphological variation that might be stratigraphically related.

Plate 24

Ochetes cf. *placentula* (Desor)

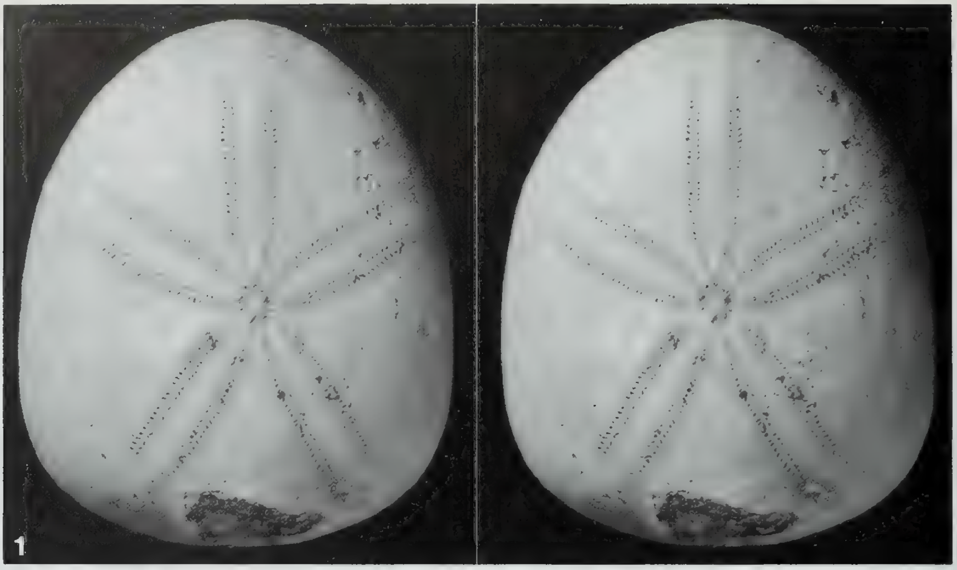
Figs 1–4 E.80644: 1, apical; 2, lateral, anterior to right; 3, posterior; 4, oral. Basal Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 5·5).

Ochetes morrisii (Forbes)

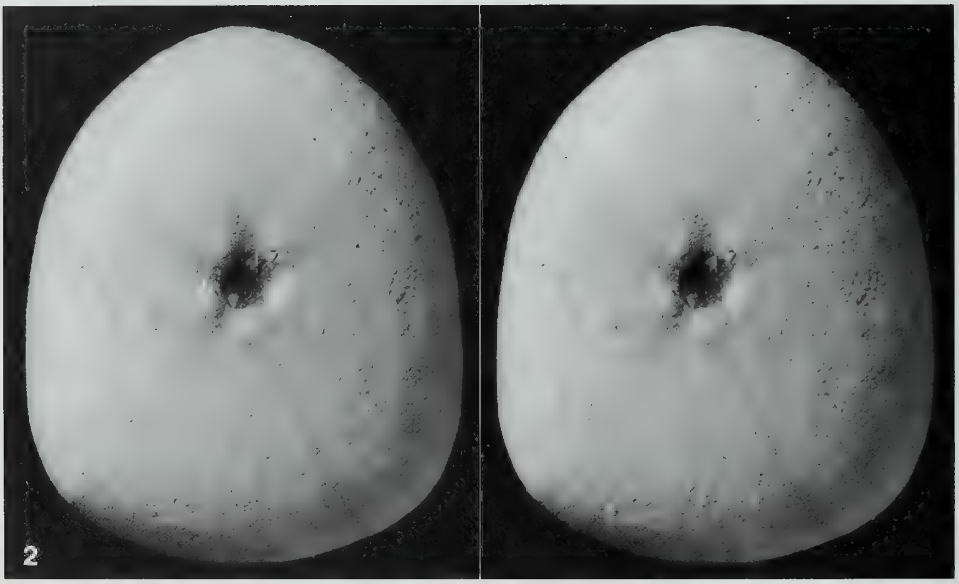
Fig. 5 E.32387, oral. Upper Greensand, Warminster, Wiltshire (× 6).

Echinogalerus rostratus (Desor)

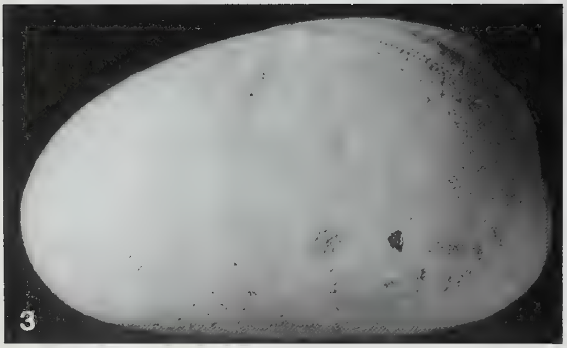
Figs 6, 7 E.80942, non-rostrate, stratigraphically low form: 6, lateral, anterior to left; 7, posterior. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 11). See also Pl. 23, fig. 4.



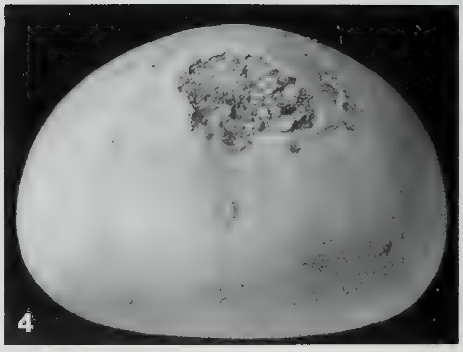
1



2



3



4

Stratigraphical occurrence and distribution. At Wilmington *C. columbarius* occurs throughout most of the succession, from 42 cm to 1020 cm below standard datum. However, it is only common at around the top of the Wilmington Sands and the base of the Grizzle, where it is abundant. This species therefore occurs throughout the *M. mantelli* Zone and also continues into the *A. rhotomagense* Zone of the Cenomanian. It is a relatively common species in the Cenomanian of England and is known from the Warminster district, and south Devon and Dorset coastal sections.

Description. *SIZE AND SHAPE.* Specimens range in size from 5·7 to almost 30 mm in length. The height of the test is 59–72% of the length (mean = 67%; SD = 3·4; N = 40), the highest point of the test being situated slightly posterior of the midline. The distance from the anterior to the highest point on the test is on average 58% of the length of the test (SD = 5·2, N = 40). In outline the ambitus of the test is vaguely egg-shaped with a roundly pointed anterior and a more truncated posterior. The test width is 78–88% of the length (mean = 83%; SD = 2·6; N = 40) and the widest part of the test lies approximately $\frac{2}{3}$ of the length from the anterior (mean = 61%; SD = 5·2; N = 40).

In profile the anterior edge is gently rounded whereas the posterior is truncated and there is a slight dorsal lip above the periproct. The ambitus is relatively low, at about $\frac{1}{3}$ of the height of the test. The adoral surface is more or less flat or very slightly convex. The dorsal surface is weakly convex and tends to be generally flattened in large and broad specimens. There is no aboral keel in the posterior interambulacrum.

APICAL SYSTEM. This is tetrabasal and lies a little anterior of centre, 34–50% of test length from the anterior (mean = 44%, SD = 3·4, N = 39). The madreporite is a large plate with many small pores; the other genital plates are considerably smaller (Fig. 47). The anterior two gonopores are more or less level. The posterior two genital plates do not touch, but are separated by ocular V. Ocular V is larger than ocular I and is in contact with the madreporite (unlike ocular I). The gonopores are large and circular and occupy most of the surface of genital plates 1, 2 and 4. There is often a distinct rim round the gonopores. Gonopores are absent in specimens smaller than about 11–14 mm in length. The precise size at which gonopores appear is variable; some specimens have gonopores by 10·5 mm, others have no gonopores at 11·8 mm. There is no evidence of sexual dimorphism.

AMBULACRA. Ambulacra are narrow relative to the interambulacra, being in width only 8–11% of the test length at the ambitus. There are 46 plates per column in the anterior ambulacrum at 5·6 mm test length, rising 83 by 19·6 mm test length (Fig. 46). All ambulacral pores are double. On the aboral surface petals are present in all five ambulacra. The petals are flush with the test surface, parallel-sided and with an unconstricted open end adambitally. The petal pores are anisopores with an elongate and oblique adradial pore and a circular perradial pore. No petals have developed in a juvenile 5·7 mm in length, but there are 17 anisopores per column at 9 mm length and 38 by 25 mm length. The anterior and the two posterior ambulacra have petals of similar length and pore-number at any particular size, but the lateral petals are always slightly shorter and with slightly fewer pores. The poriferous zone forms 40–50% of the plate width in the petals. Ambulacral plates are always simple and are short and elongate. The length of the petals is about 70% of the length from the apex to the ambitus viewed from above.

Below the petals the ambulacral plates are squarish. Ambulacral pores are very small and insignificant partitioned isopores situated in the adoral/adradial corner of each plate and set obliquely.

Plate 25

Catopygus columbarius (Lamarck)

Figs 1–4 E.80657, form from basal part of section corresponding to *C. carinatus* of Goldfuss: 1, apical; 2, oral; 3, lateral; 4, posterior. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 4).

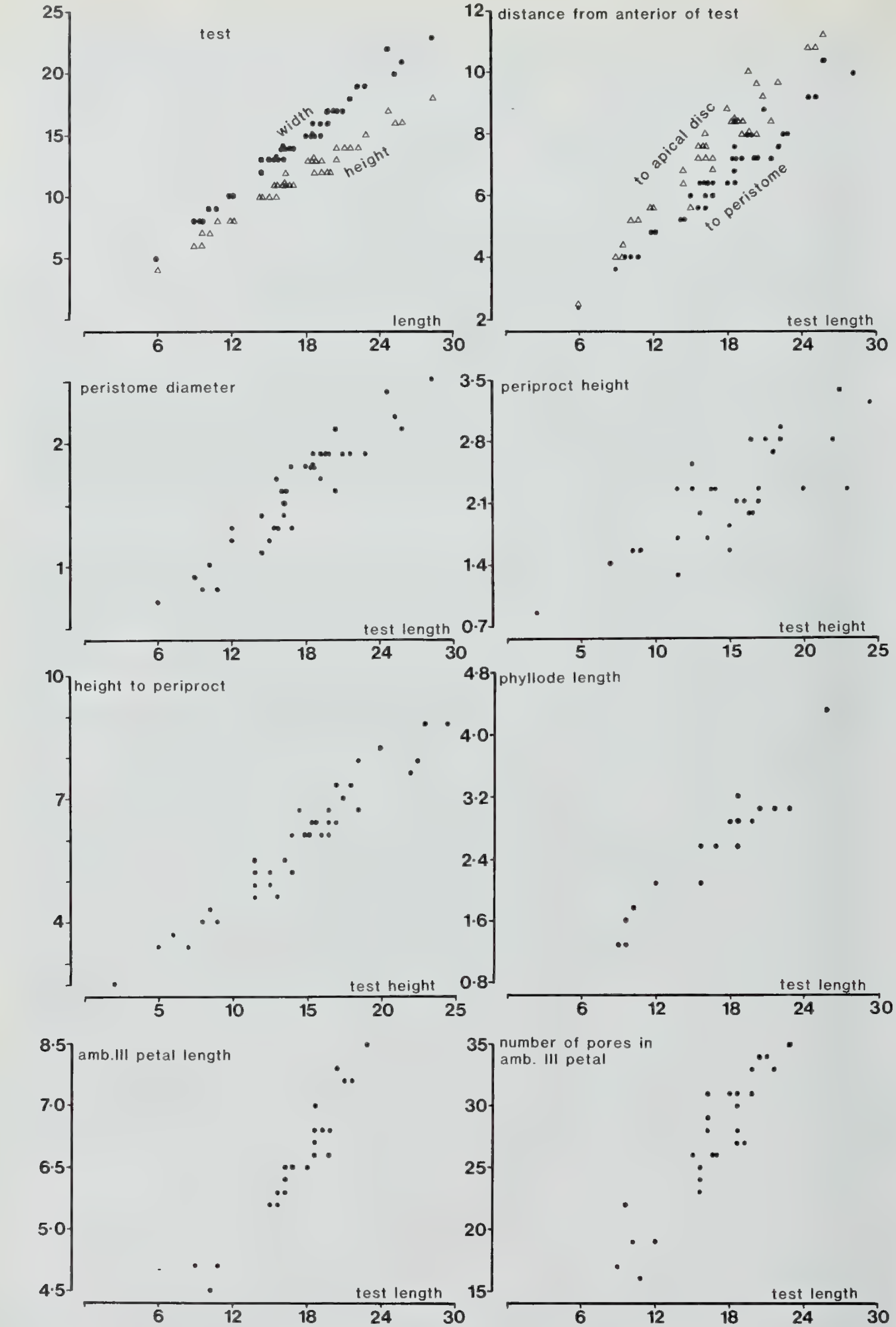


Fig. 46 Biometric data on *Catopygus columbarius* from the Lower Cenomanian of Wilmington.

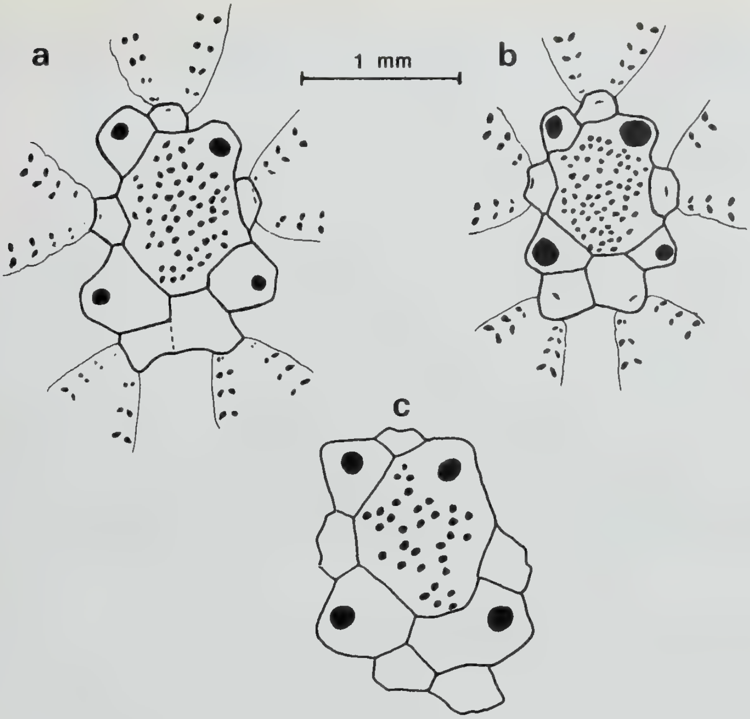


Fig. 47 Camera lucida drawings of apical disc plating in *Catopygus columbarius* from the Lower Cenomanian of Wilmington: a, E.80695; b, E.80675; c, E.80689. Ocular plate III to the top.

Adorally the ambulacra are broadened to form phyllodes (Fig. 48), in each of which there are four columns of pores. The inner series consist of four pores per column in the anterior phyllode but five in the other phyllodes. The outer series consists of eight to ten pores. All phyllode pores are anisopores with a large circular adradial pore and a small slit-like perradial pore. These anisopores are set strongly oblique so that the perradial pore lies more or less adoral to the adradial pore. No buccal pores are present and the phyllode pores do not extend into the well that leads into the peristome but end at the outer edge of the bourrelets. Ambulacra end at the peristome in a pair of large L-shaped plates back-to-back. These are followed by a narrow zone of quadriserial plating which gives way to occluded pseudocompounding. At the adambital end of the phyllodes ambulacral plating becomes simple.

INTERAMBULACRA. These are relatively broad and individual plates are very slightly kinked. There are 15 or 16 plates per column at 5–10 mm test length, rising to 19 plates by about 20 mm test length. At the adoral end each interambulacrum ends in a single swollen plate which forms the bourrelet and the well to the peristome (Fig. 49). The plates immediately adjacent to this most proximal plate are particularly small. Plating in the posterior interambulacrum is identical to that in all the other interambulacra.

FLOSCELLE. Bourrelets are well developed and in all specimens larger than about 1 cm in length the 10 ambulacral and 5 interambulacral plates bounding the peristome are heavily tuberculate. The interambulacral plates are swollen to form five elliptical ridges adjacent to the peristome whereas the ambulacra are flush or very slightly sunken. The bourrelets are not present in an individual 5·6 mm in length and are slightly swollen with just two rows of dense tubercles at 9·2 mm in length. Phyllodes are relatively short. The anterior and the two posterior phyllodes extend only about a third of the distance from the peristome to the ambitus, whereas the lateral phyllodes extend about half of the length.

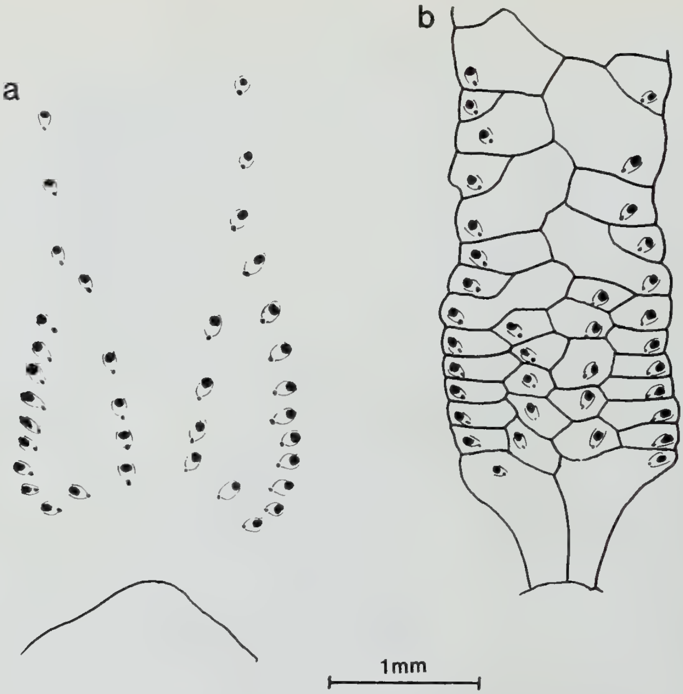


Fig. 48 Camera lucida drawing of phyllode pore arrangement and ambulacral plating in *Catopygus columbarius* (E.80665) from the Lower Cenomanian of Wilmington. The edge of the peristome is to the bottom.

PERISTOME. The peristome is small and weakly sunken and is surrounded by a prominent floscelle. In length the peristome is only 8–12% of the test length (mean = 9%; SD = 1·0; N = 37). At 5·6 mm length the peristome is circular in outline, at 9 mm length it is pentagonal and between 14 and 30 mm length the peristome is slightly wider than long. The peristome lies anterior of the midline, 34–43% of the length from the anterior (mean = 38%; SD = 2·6; N = 40).

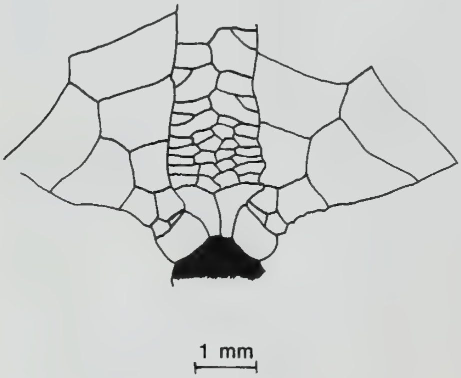


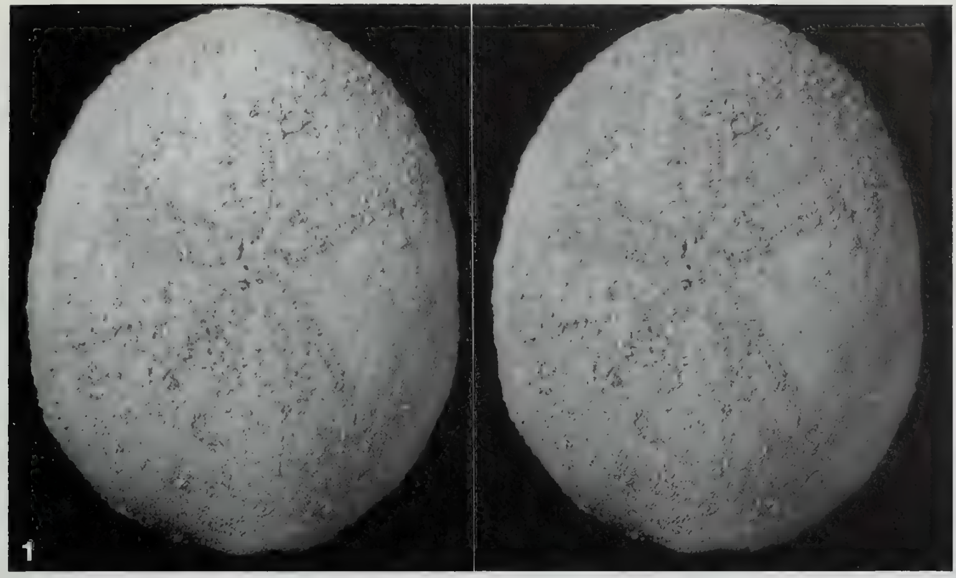
Fig. 49 Camera lucida drawing of oral plating in *Catopygus columbarius* (E.80686) from the Lower Cenomanian of Wilmington. Peristome to the base.

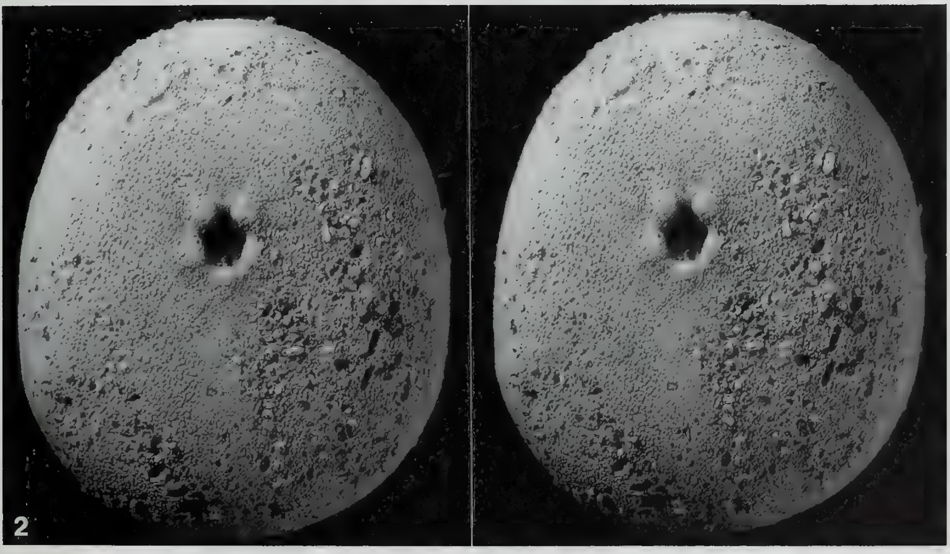
Plate 26

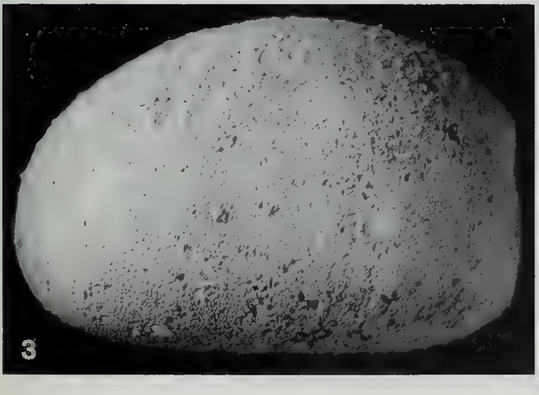
Catopygus columbarius (Lamarck)

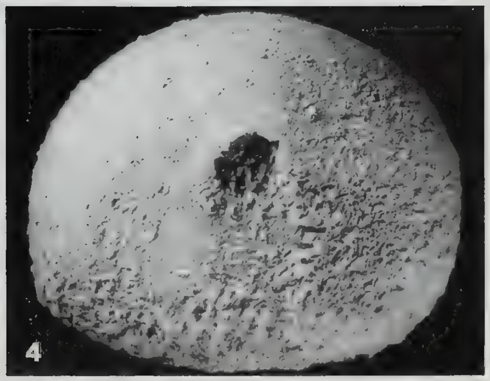
Figs 1, 4 E.80706: 1, apical; 4, posterior. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (×4).

Figs 2, 3 E.80830: 2, oral; 3, lateral. As last (×3).


1


2


3


4

PERIPROCT. The periproct is situated on the steep posterior surface and is hardly visible from above. It is surrounded by a small rim which is best developed aborally. The periproct is relatively small, only 14–22% of the test height (mean = 18%; SD = 2·8; N = 32). It is taller than wide, with a width around 50–75% of the height. The periproct is situated slightly above mid-height and the base of the periproct lies 44–59% of the test height above the base of the test (mean = 51%; SD = 4·1; N = 39). The periproct lies between interambulacral plates 10, 11 and 12 and in all specimens there are 9 interambulacral plates per column between the periproct and peristome.

TUBERCULATION. All tubercles in this species are small and inconspicuous. Aboral tubercles are small, measuring about 0·2 mm in diameter, and fairly dense, with about 5 tubercles per mm^2. The tubercles are perforate with a more or less circular areole. They are scattered irregularly over the plates and the primary tubercles are ringed by miliary tubercles. Tuberculation is uniform over the entire dorsal surface. At the ambitus, tubercles become noticeably larger and oral tubercles are twice the diameter (0·4 mm) of dorsal tubercles. There are about 4 tubercles per mm^2. All tubercles are perforate and crenulate and slightly sunken. They are surrounded by a ring of miliaries, which are in two distinct sizes. There is a narrow, sparsely tuberculate zone in the posterior interambulacrum, where only miliary tubercles are present.

Tubercles are largest laterally in the subambital region and decrease towards the peristome. No apparent areole enlargement is visible in any of the oral tubercles which, apart from the posterior naked zone, are more or less uniform.

Around the peristome there is very dense tuberculation for the food-manipulating spines.

REMARKS. *Catopygus columbarius* was first figured and named by Parkinson (1811) who unfortunately used the preoccupied name *Echinites pyriformis*. The name *Nucleolites columbaria* was first proposed by Lamarck (1816), who gave no figure and only the briefest of diagnoses. Although this species was often referred to by later workers, it was not figured until d'Archiac (1847: 296–7; pl. 13, figs 3, 3a–c) redescribed it. After *C. columbarius* was described but before it was figured, Goldfuss (1829) described and figured a species of *Catopygus* under the name *Nucleolites carinatus*. Both d'Orbigny (1856) and Wright (1875) considered *N. columbaria* and *N. carinatus* to be synonymous. However, Cotteau (*in* d'Orbigny 1856: 439) and Cotteau & Triger (1859) treated them as valid and discrete species on the basis that *C. columbarius* was larger, narrower anteriorly and rather more enlarged posteriorly, more arched adapically in profile, lacked a carina and had the anus a little less elevated than in *C. carinatus*. The specimen figured by Goldfuss is very distinct in having in outline a broad and truncated posterior, whereas specimens figured under the name *C. columbarius* are more ovoid in outline, coming to a distinct point posteriorly.

Both forms of *Catopygus* are found at Wilmington (Fig. 12, p. 34), although the majority conform to the *C. columbarius* type. Although most specimens can be placed in one or other group there are a small number of intermediates which are difficult to assign. *C. carinatus* forms dominate in the lowest part of the succession but are absent throughout most of the Wilmington Sands and Grizzle. The only specimen collected from the Middle Cenomanian Wilmington Limestone is closer to *C. carinatus* in form. The two forms are identical in all structural details and differ only in general shape. As the differences are minor and intermediates exist I prefer to place them all within one variable species, *C. columbarius*. Occasional highly cylindrical forms of *C. columbarius* are also found at Wilmington and Agassiz & Desor's (1847) species *Catopygus cylindricus* appears to be no more than an unusually elongate *C. columbarius*.

Family **CASSIDULIDAE** Agassiz & Desor, 1847

Genus ***OCHETES*** Pomel, 1883

Ochetes cf. ***placentula*** (Desor 1857)

Pl. 24, figs 1–4

cf. 1857 *Echinobrissus placentula* Desor: 269.
cf. 1869 *Echinobrissus subquadratus* de Loriol *in* Loriol & Gillieron: 43; pl. 6, fig. 1 [*non* d'Orbigny].
cf. 1873 *Echinobrissus placentula* Desor; de Loriol: 269; pl. 21, figs 12–14.

Material. A single specimen tentatively placed in this species (E.80644) was collected at Wilmington. As it is not particularly well preserved the following description is brief.

Stratigraphical occurrence. The Wilmington specimen comes from the coarse glauconitic greensands exposed at the very base of the quarry, 1020 cm below standard datum level. It thus comes from a horizon low in the Lower Cenomanian.

Description. *SIZE AND SHAPE.* The test is 11·3 mm in length and 9·4 mm in breadth, which is 83% of the length. In outline it has a rounded anterior, almost parallel-sided lateral margins and a tapered and truncated posterior (Pl. 24, figs 1–4). The oral surface is noticeably concave and the lateral margins are relatively sharp and make an acute angle with the oral face. The ambitus lies very close to the base of the test. The widest point on the test lies 53% of the test length from the anterior. In profile the test is low and shaped like a slipper, with a convex base, a fairly sharp anterior angle and a gently sloping dorsal region anterior to the apex. The test height is 37% of the length and the tallest point on the test lies 53% of the test length from the anterior border. The posterior 40% of the dorsal surface of the test is concave and in profile appears to be cut away. Viewed from the posterior the test is crescentic in outline, with a convex upper surface and a concave lower surface.

APICAL SYSTEM. Plate arrangement of the apical disc is unknown. The anterior border of the apical disc lies 44% of the test length from the anterior border of the test.

AMBULACRA. Adapically the ambulacra are flush, narrow and non-petaloid. Ambulacral pores in all five ambulacra are identical. They are minute, circumflexed isopores with a narrow interporal partition and are non-conjugate. These pores are not particularly closely packed and are very difficult to locate with the naked eye. On the oral surface there are broad phyllodes apparently with only a single column of ambulacral pores on each side but the detailed plating arrangement and pore structure cannot be determined.

INTERAMBULACRA. Interambulacral zones are relatively broad. Small bourrelets are present around the peristome, but once again the details of this area cannot be made out. Plate arrangement and number are unknown.

PERIPROCT. The periproct is large and clearly visible from above. It is triangular in outline, tapering adapically and towards the anterior, and opening posteriorly into a slight anal sulcus that leads to the posterior margin. The anterior edge of the periproct lies 61% of the test length from the anterior border. The height of the periproctal opening is 48% of the test height and, at its broadest, the periproct is as broad as it is tall.

PERISTOME. This is more or less circular in outline, though very slightly longer than broad. The length of the peristome is 12% of the test length and its width is 93% of its length. Its anterior edge lies 36% of the test length from the anterior border of the test.

TUBERCULATION. Only aboral tubercles are sufficiently well preserved to be described. These are small, uniformly-sized and moderately densely packed. The tubercles are slightly sunken and adjacent rows are separated by a single row of miliaries set on the narrow rim. Oral tubercles are large and there appears to be a broad median naked zone.

Remarks. The position and shape of the periproct, the non-petaloid ambulacra and in particular the highly distinctive shape of the test with its sharp, thin ambitus and uniformly concave oral surface place this species in the genus *Ochetes* Pomel. Kier (1962) defined this genus and designated *Nucleolites morrisii* Forbes the type species; he included no other species. *Ochetes morrisii* was first described by Forbes (1849), who gave only a brief diagnosis: no figure appeared until Kier (1962) published some excellent photographs. (The *Echinobrissus Morrisii* figured and described by d'Orbigny (1854) and Wright (1882) are not the same and appear to be specimens of *Nucleopygus.*) In comparison with *O. morrisii* the Wilmington specimen is noticeably shorter and squatter in outline (compare Pl. 24, figs 1–4 with fig. 5). A sample of *O. morrisii* from Warminster (E.32386–8, E.42410–2, E.42414–5) have a width to length ratio of 0·73 to 0·78 (mean = 0·75; SD = 0·02; N = 8) whereas the same ratio in the Wilmington specimen is 0·83.

The Wilmington specimen appears to be identical with the specimens figured by de Loriol (1873) as *Echinobrissus placentula.* This species, which was first briefly described by Desor

(1857), is known from the uppermost Aptian of France and Switzerland. Because of the difference in their age and because I have not examined the types of the species, the Wilmington specimen is only tentatively placed in it.

Order **HOLASTEROIDA** Durham & Melville, 1957

Family **HOLASTERIDAE** Pictet, 1857

Genus ***HOLASTER*** Agassiz, 1836

Holaster nodulosus (Goldfuss 1829)

Pl. 27, figs 1–4; Pl. 28, figs 1–6; Figs 50, 51, 52b–d, 53, 54c–d

1829 *Spatangus nodulosus* Goldfuss: 139; pl. 45, fig. 6.
1854 *Holaster laevis* d'Orbigny: 83; pl. 812, figs 1–8 [*non* Agassiz].
1854 *Holaster carinatus* d'Orbigny: 105; pl. 818, figs 1–7 [*non* Lamarck].
1859 *Holaster carinatus* Agassiz; Cotteau & Triger: 195; pl. 24, figs 3–5.
1865 *Holaster carinatus* Agassiz; Cotteau: pl. 69, figs 3–7.
1873 *Holaster laevis* de Luc; de Loriol: 319 [*partim*]; pl. 27, fig. 1 only.
1878 *Holaster laevis* Wright: 310; pl. 72, fig. 1 [*non* Agassiz].
1894 *Holaster nodulosus* (Goldfuss) Lambert: 60.
1917 *Holaster nodulosus* (Goldfuss); Lambert: 203.
1924 *Holaster nodulosus* (Goldfuss); Lambert & Thiéry: 401.
1935 *Holaster nodulosus* (Goldfuss); Smiser: 66; pl. 7, fig. 2.
1963 *Holaster nodulosus* (Goldfuss); Cayeux: 20; fig. 5.

MATERIAL. This species is abundant at Wilmington and a large number of specimens were collected *in situ*. A biometric analysis was carried out on 31 specimens from Wilmington (E.80302, E.80309–10, E.80318, E.80321–2, E.80388, E.80430, E.80465, E.80496, E.80512, E.80529, E.80543, E.80563, E.80565, E.80574, E.80576, E.80604–17).

STRATIGRAPHICAL OCCURRENCE AND DISTRIBUTION. At Wilmington the species occurs throughout the Wilmington Sands and Grizzle, from 926 cm to 86 cm below standard datum. It is most abundant between 600 and 200 cm below standard datum (Fig. 7, pp. 18–19). It comes from the Lower Cenomanian and is a common species at this level in both England and throughout north-western Europe.

DESCRIPTION. *SIZE AND SHAPE.* In outline the test is weakly cordate and slightly longer than broad. There is a very feeble frontal notch, on average only 2–3% of the test length (mean = 2·5%; SD = 1·1; N = 31) in depth at the ambitus, and adapically the anterior ambulacrum becomes flush with the adjacent interambulacra. No carinae are developed and the test tapers posteriorly to a rounded point. Tests range in size from 16·7 to 48·2 mm in length (mean = 28·0 mm; SD = 7·5; N = 31). Test width is 87–97% of the test length (mean = 93%; SD = 2·2; N = 31) and the widest point on the test lies 40–56% of the test length from the anterior border of the test (mean = 47%; SD = 3·8; N = 31). The height of the test is 53–67% of the test length (mean = 60%; SD = 4·0; N = 31) and the tallest point on the test lies just posterior of the apical disc, 55–71% of the test length from the anterior border (mean = 63%; SD = 4·8; N = 31). In profile the base is flat or slightly convex, and the apical surface is broad and slightly vaulted. The posterior of the test is more or less vertically truncated whereas the anterior is convex and slopes posteriorly (Fig. 51). The ambitus lies close to the base of the test, about 12–25% of the test height above the base of the test. The plastron is very slightly keeled.

APICAL SYSTEM. The apical disc is typically elongate (Fig. 52b–d) and in length is 14–20% of the test length (mean = 17%; SD = 1·8; N = 24). The maximum width of the apical disc is 34–54% of its length (mean = 42%; SD = 5·2; N = 20) and the anterior edge of the apical disc lies 31–40% of the test length from the anterior border of the test (mean = 36%; SD = 2·9; N = 26). Ocular plate III is small and protrudes anteriorly. Genital plate 3 is also relatively small, but is in broad contact with ocular plate IV (Fig. 52b–d). The remaining plates are broadly similar in size except for the posterior two oculars, which are slightly smaller. Genital pores are relatively small and situated near the outer border of each genital plate.

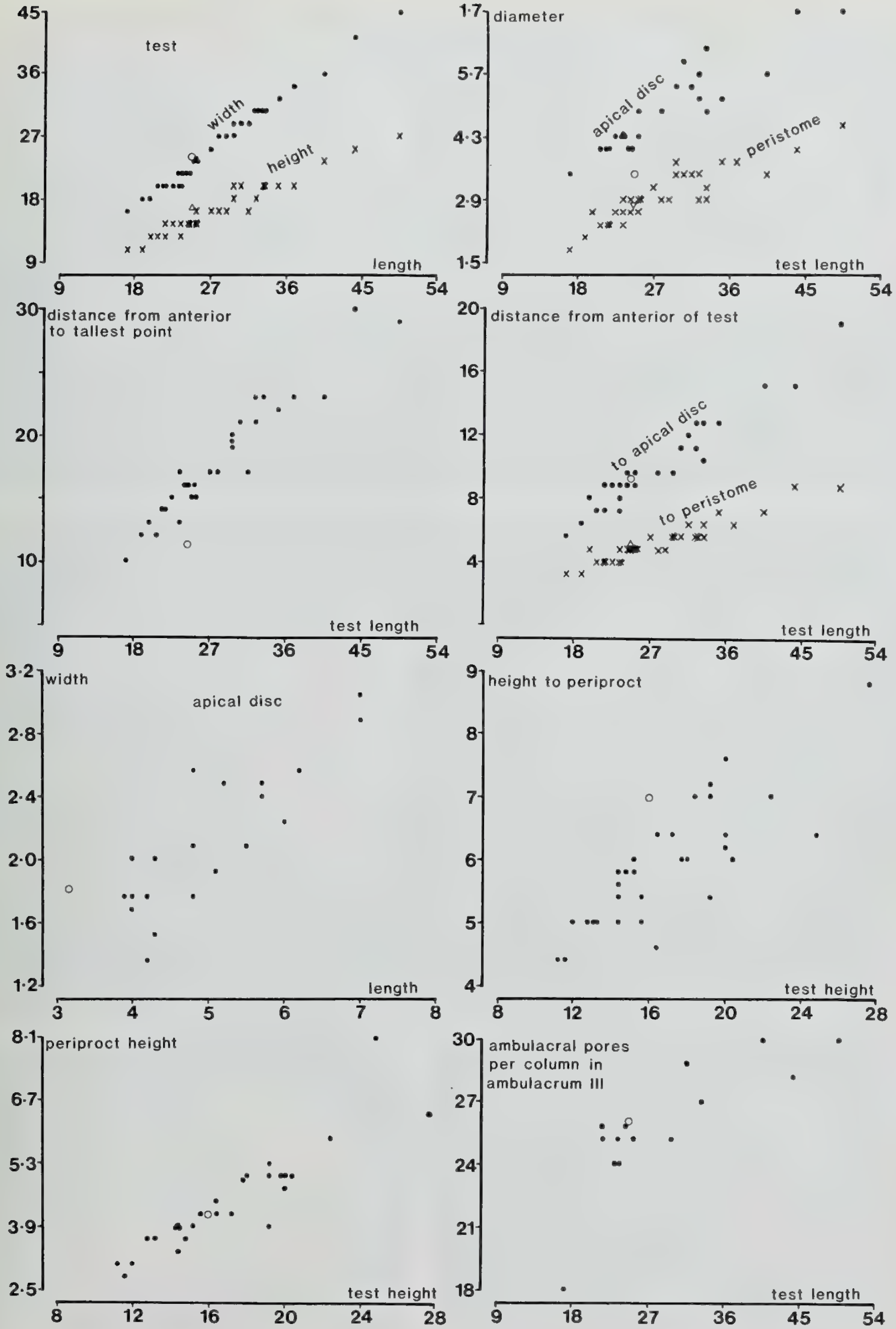
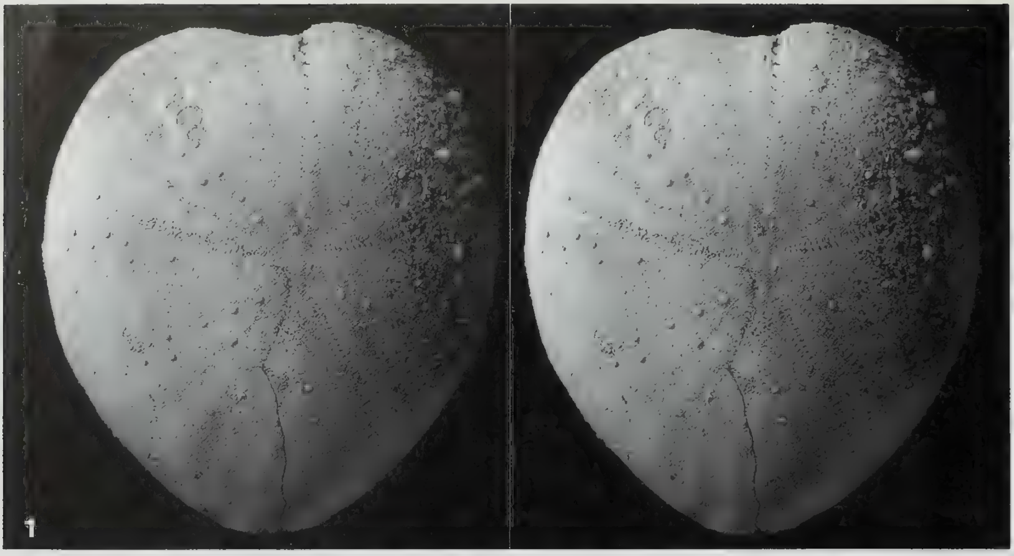
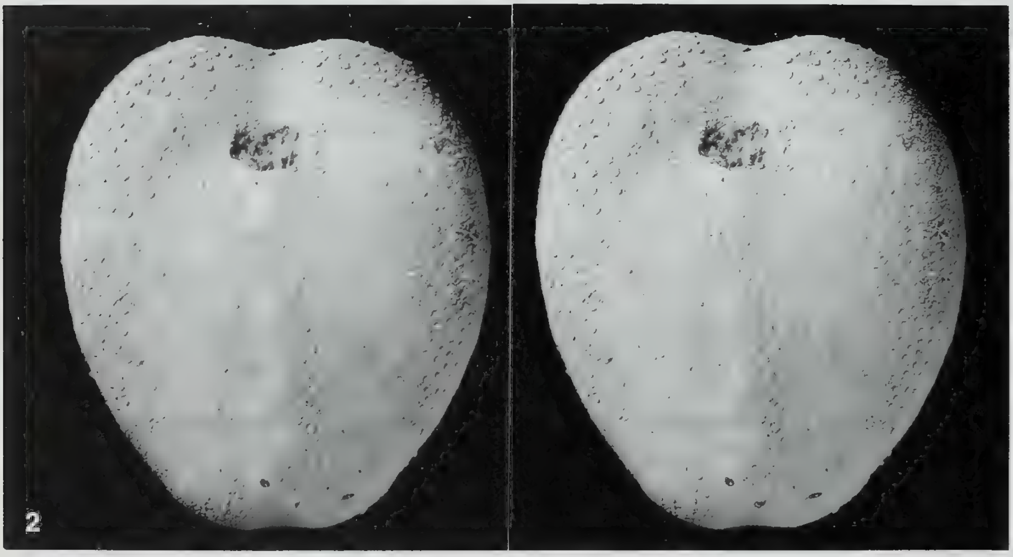


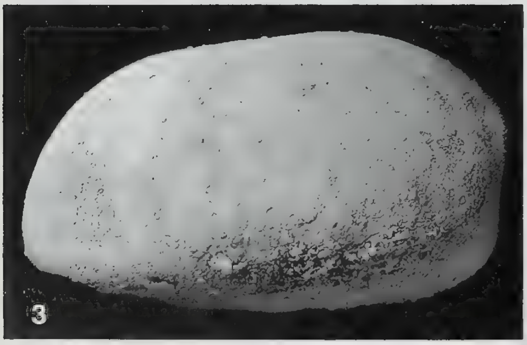
Fig. 50 Biometric data on *Holaster nodulosus* (●, X) and *H. laevis* (△, ○) from the Lower Cenomanian of Wilmington.



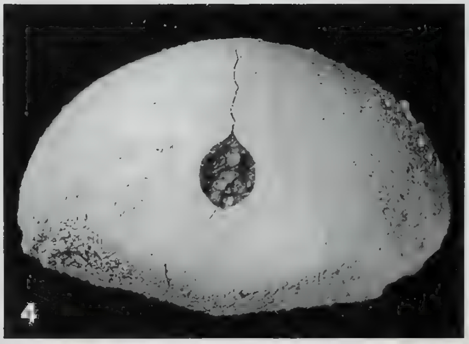
1



2



3



4

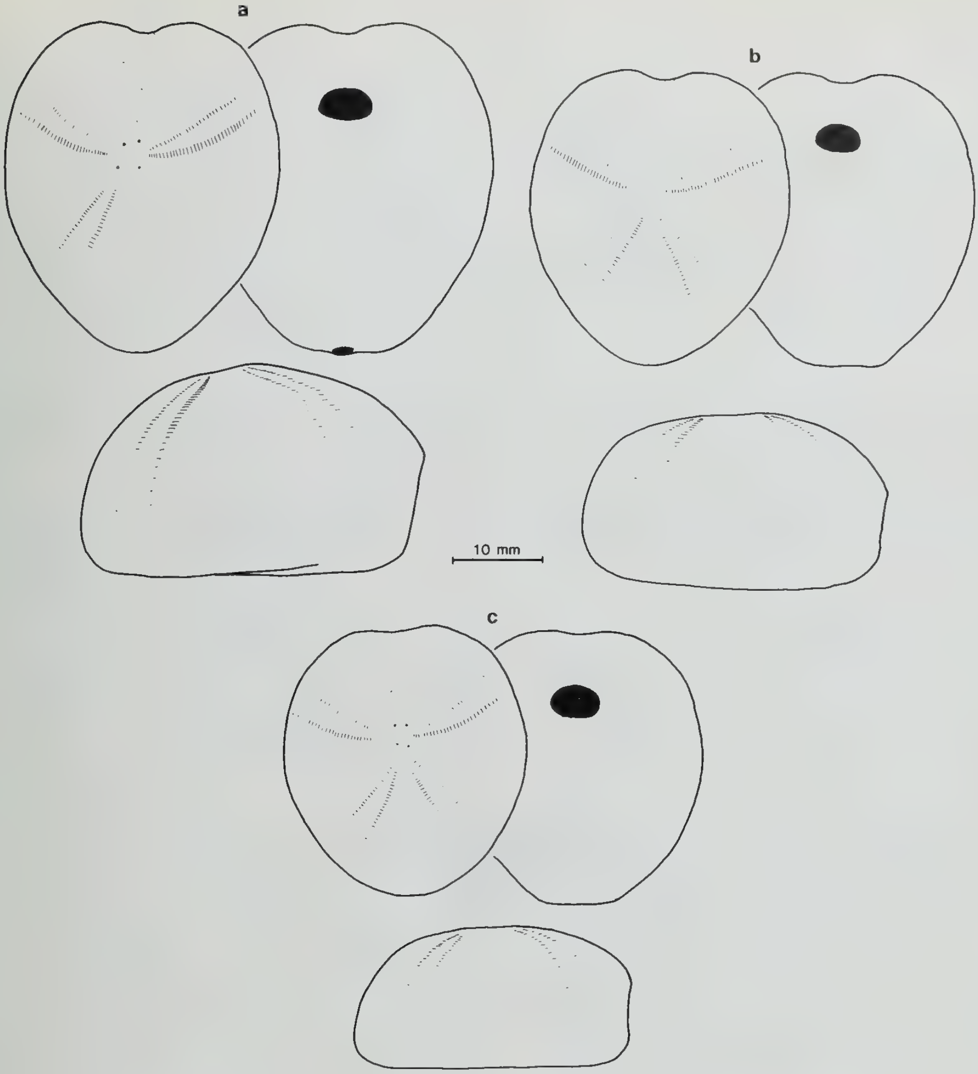


Fig. 51 Outline drawings of shape varieties of *Holaster nodulosus* from the Cenomanian at Wilmington: a, E.80619, tall form; b, E.80613, typical form; c, E.80318, flat form.

AMBULACRA. The paired ambulacra are lanceolate and sub-petaloid adapically, whereas the anterior ambulacrum is non-petaloid. There are 18 ambulacral pores per column in ambulacrum III at a test length of 17 mm, rising to 29 or 30 at a test length of 40 mm. The ambulacral pores are small, obliquely-orientated isopores with a narrow interporal partition and a distinct neural canal. They are fairly closely spaced adapically but become progressively

---

Plate 27
Holaster nodulosus (Goldfuss)
Figs 1, 3, 4 E.80605: 1, apical; 3, lateral, anterior to right; 4, posterior. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 2).
Fig. 2 E.80302; oral. As last (× 3).

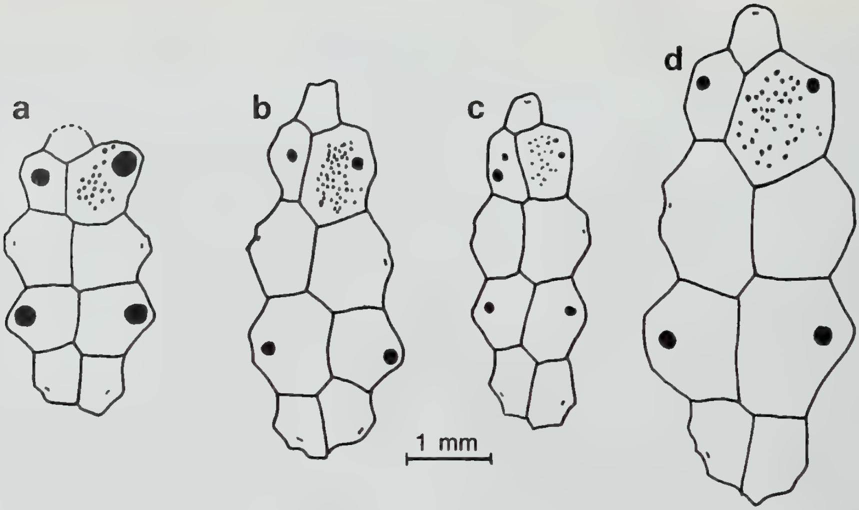


Fig. 52 Camera lucida drawings of apical disc plating of *Holaster* from Wilmington: a, *H. laevis*, E.80544; b–d, *H. nodulosus*: b, E.80611; c, E.80318; d, E.80610.

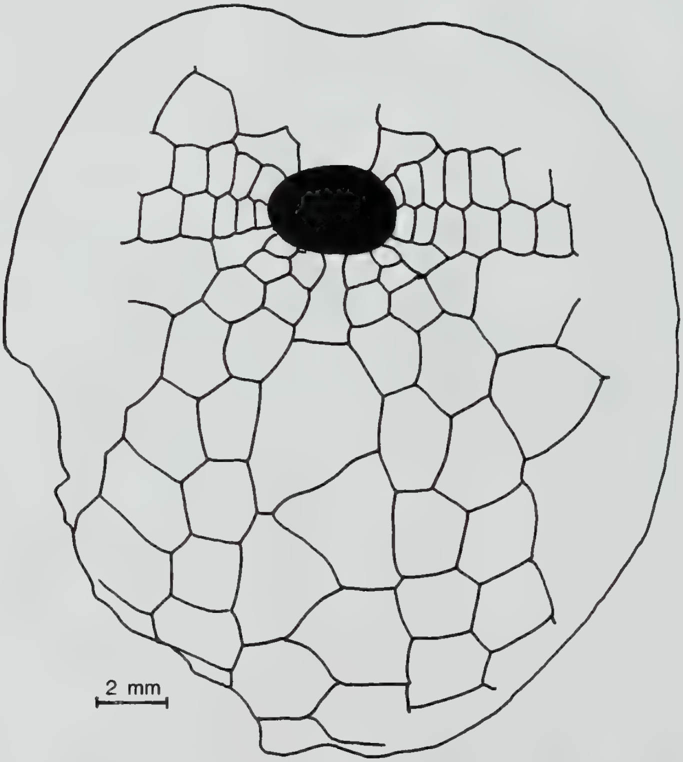


Fig. 53 Camera lucida drawing of oral plating of *Holaster nodulosus* (E.80609) from the Lower Cenomanian of Wilmington.

wider apart adambitally. They are about 0·3 mm in diameter. The three most adoral isopores in each column of ambulacrum III are noticeably larger and would have supported phyllodal tube feet.

The anterior paired ambulacra curve slightly with the concave margin anterior. The two columns of pores are very unequal adapically. The anterior column of ambulacral pores are small, circumflexed isopores generally no more than 0·3 mm in width, whereas the posterior column has isopores over twice the width (0·8 mm), in which the pores are transversely elongate and taper towards one another. They are conjugate, with a distinct groove linking the two. Broad, conjugate isopores are moderately densely packed and extend most of the length to the ambitus. Immediately above the ambitus, however, the pores decrease noticeably in size and become much more circumflex, like those of the anterior column. There are 37 pores per column in ambulacrum II at a test diameter of 24 mm, rising to about 50 at a test diameter of 49 mm.

Ambulacral pores in the posterior paired ambulacra are very similar, although here the two columns of pores are almost, but not quite, identical in width. Individual isopores are conjugate and slightly circumflex, and are 0·6 mm in width in the posterior column and 0·5 mm in width in the anterior column. They extend about $\frac{3}{4}$ of the distance to the ambitus, where the pores become gradually smaller and more circumflexed. In both the anterior and posterior petals there is no sharp, clear-cut base to the zone of respiratory tube feet. The perradial interporal zone is relatively broad in all ambulacra and is at least twice the breadth of the poriferous zone, and sometimes almost three times.

Ambitally and subambitally the ambulacral pores are small and difficult to distinguish but remain isopores. Adjacent to the peristome, however, larger isopores with a circular attachment rim and a raised interporal partition are found. There are three such pores per column in the anterior ambulacrum, seven in the lateral paired ambulacra and four or five in the posterior paired ambulacra.

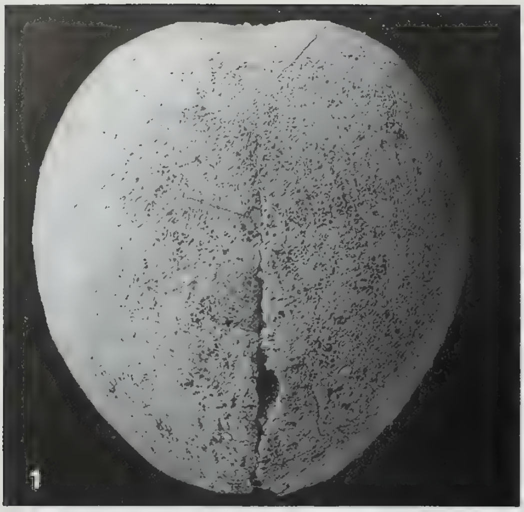
INTERAMBULACRA. The anterior ambulacra are smoothly rounded on either side of the frontal groove, without the slightest hint of carinae. The aboral surface behind the apical disc is also non-carinate.

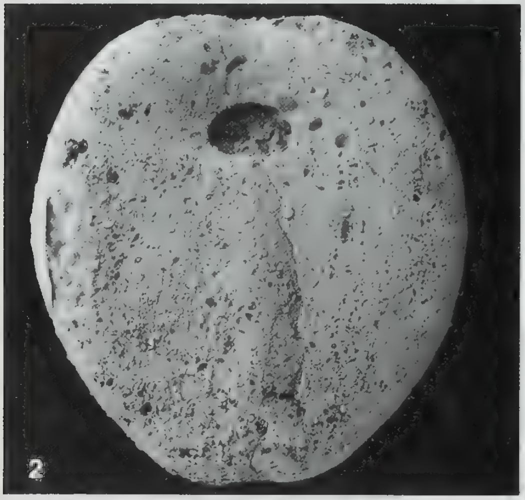
On the oral surface the posterior interambulacrum is long and narrow, and is approximately parallel-sided for much of its length, only tapering close to the peristome (Fig. 53). The labrum is longer than broad and wedge-shaped in outline, with a straight posterior border. It extends for 17–18% of the distance from the peristome to the posterior border. Plate 2a, which follows the labrum, is considerably larger than all succeeding interambulacral plates and is less triangular in outline. The plastron is composed of the labrum together with plates 2a, 2b to 4a, 4b. The periproct lies between plates 7a, 7b and 9a, 9b.

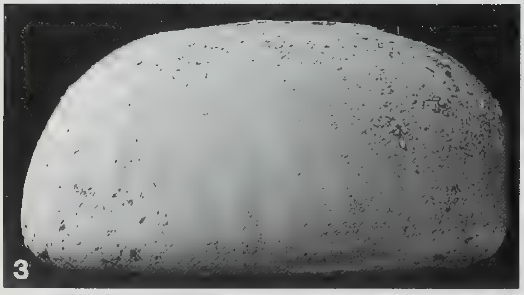
PERIPROCT. This lies at the top of the posterior face and faces slightly adorally. It is oval in outline, being taller than broad and has a rounded adoral edge and a slightly more pointed adapical edge. The height of the periproct is 18–33% of the test height (mean = 25%; SD = 2·6; N = 27) and its width is 69–86% of its height (mean = 76%; SD = 4·0; N = 25). The base of the periproct lies 27–49% of the test height above the base of the test (mean = 37%; SD = 4·5; N = 78).

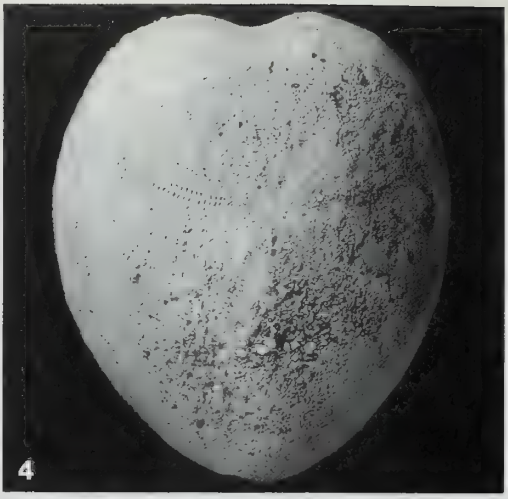
PERISTOME. The peristome is wider than long and oval in outline. The labral plate does not project over the peristome and the posterior border of the periproct is convex. Its length is 11–19% of the test length (mean = 16%; SD = 1·5; N = 31) and its width 1·2–1·7 times its length (mean = 1·4; SD = 0·1; N = 31). The anterior edge of the peristome lies 16–24% of the test length from the anterior border of the test (mean = 19%; SD = 1·9; N = 31). The peristome is either completely flush with the oral surface or very slightly sunken around its anterior border so as to face very slightly anteriorly.

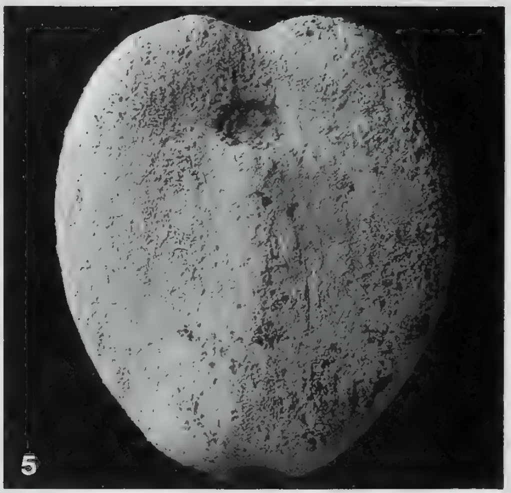
TUBERCULATION. Aboral tuberculation is distinctly heterogeneous, with one or two large primary tubercles on most interambulacral plates. These have a circular areole and a crenulate platform, but with a ridge developed on the posterior side of the mamelon. In the anterior interambulacra the anterior columns have no primary tubercles although adjacent to the frontal ambulacrum there is an adapical zone of very slightly larger and more densely-











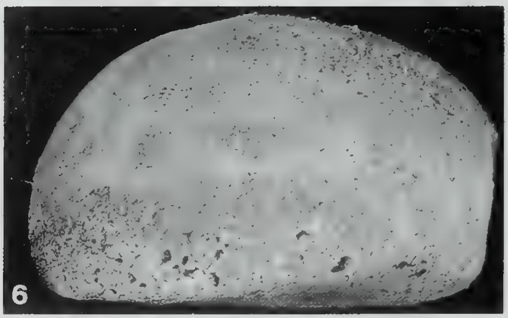


Plate 28

Holaster nodulosus (Goldfuss)

Figs 1–3 E.80318, depressed, stratigraphically high form: 1, apical; 2, oral; 3, lateral, anterior to left. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 2).

Figs 4–6 E.80619, tall form: 1, apical; 2, oral; 3, lateral, anterior to left. As last (× 2).

packed tubercles, about 0·3 mm in diameter. This tuberculation is lost adambitally. In the posterior columns the first two adapical plates have only small tubercles, while the following two plates each have a single primary tubercle, about 1 mm in diameter and lying near the adradial suture. The next four plates also have a large primary tubercle but in addition have a slightly smaller secondary tubercle positioned more interradially. The primary tubercles tend to become slightly smaller away from the apical zone.

In lateral interambulacra there is also a difference in tuberculation between anterior and posterior columns. In the anterior column the five most adapical plates have only small scattered tubercles. There is a single large primary on the next plate and the two succeeding plates have both a large primary tubercle and a smaller, more interradial, secondary tubercle. In some specimens the succeeding plate may also have a primary tubercle. In the posterior column, however, only the first two adapical plates lack primary tubercles. The next two plates each have a single large primary tubercle while the next plate has both a primary and a more interradial secondary tubercle. The more adambital plates have only a scattering of small tubercles.

In the posterior interambulacrum the three most adapical plates have a large tubercle lying close to the interradial suture and may also have a smaller secondary tubercle closer to the adradial suture. Close to the periproct the plates have only small tubercles.

Over the rest of the dorsal surface there is a sparse scattering of small crenulate tubercles about 0·25 mm in diameter, with interspersed miliary tubercles. This tuberculation continues without any change across ambulacral areas including the frontal ambulacrum.

On the oral surface, plastron tuberculation is moderately dense and continues right to the peristome. There are very few miliary tubercles in between. Periplastronal areas are very broad and devoid of tubercles making the oral surface appear rather sparsely tuberculate.

Remarks. This species was first described by Goldfuss (1829) who gave a brief diagnosis and a reasonable figure, but it was for a long time confused with *H. laevis* (Brongniart) and *H.*

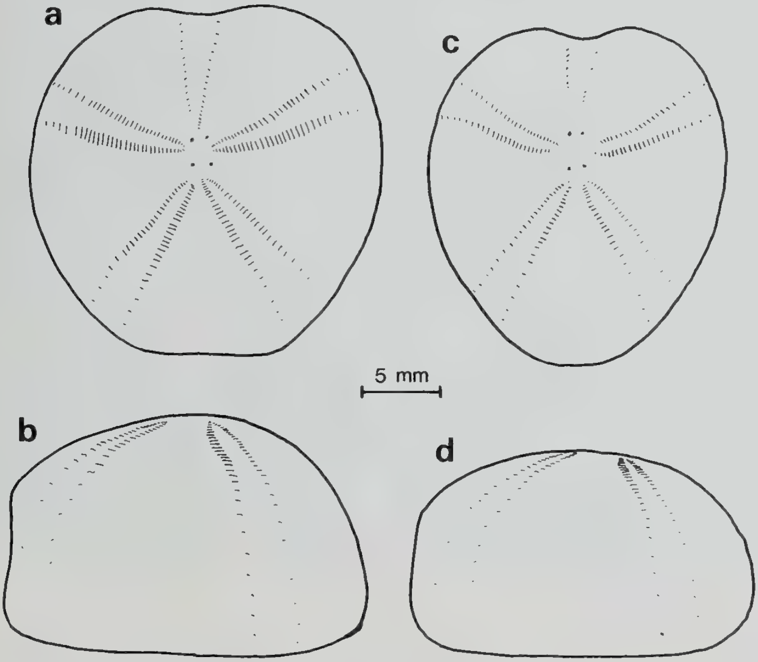


Fig. 54 Outline drawings of: a, b, *Holaster laevis* (E.80617), and c, d, *H. nodulosus* (E.80544), from the Lower Cenomanian of Wilmington, showing their different overall form.

carinatus (Lamarck). *H. nodulosus* differs from *H. laevis* in being longer than broad and tapering posteriorly to a rounded point. In *H. nodulosus* the plastron is more elongate and parallel-sided, with a long tapering labrum and an enlarged succeeding plate 2a, compared with *H. laevis*. *H. carinatus* Lamarck is a *nomen dubium* based on an internal mould of an indeterminable species.

There is a great deal of variation in this species, particularly in profile of the test. The large sample available shows that there is continuous gradation between very distinct end members, a variation which is not related to stratigraphical position. At one end there are a few tall, domal forms (Pl. 28, figs 4–6), while at the other there are low, flat-based forms with only a slightly convex dorsal surface (Pl. 28, figs 1–3). The great majority, however, have a moderately domed test profile with the apex of the test relatively far back (Pl. 27, figs 1–4). The occasional flat-topped specimen is found throughout the species range at Wilmington, but the tall variety is found only in the Grizzle.

Holaster laevis (Brongniart 1822)

Pl. 29, figs 1–4; Figs 50, 52a, 54a–b, 55

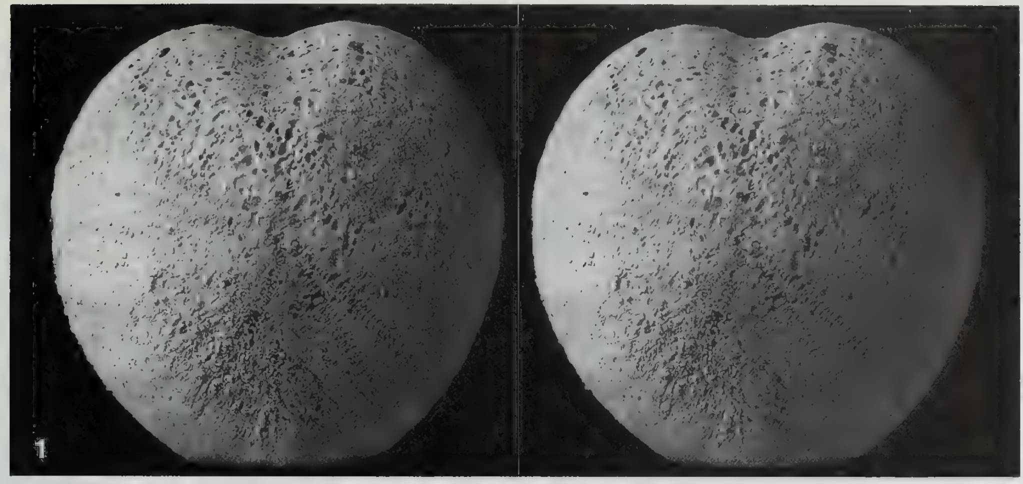
1822 *Spatangus laevis* de Luc Ms; Brongniart: 97, 399; pl. 9, fig. 12
1836 *Holaster laevis* (Brongniart) Agassiz: 183.
1836 *Holaster marginalis* Agassiz: 183.
1839 *Holaster laevis* (Brongniart); Agassiz: 17; pl. 3, figs 1–3.
?1839 *Holaster transversus* Agassiz: 18; pl. 3, figs 4, 5.
1847 *Holaster marginalis* Agassiz; Agassiz & Desor: 134.
?1847 *Holaster transversus* Agassiz; Agassiz & Desor: 134.
1854 *Holaster marginalis* Agassiz; d'Orbigny: 109; pl. 819, figs 1–6.
non 1865 *Holaster laevis* Cotteau: 83; pl. 812, figs 1–8 [= *H. nodulosus* (Goldfuss)].
1873 *Holaster laevis* (Agassiz); de Loriol: 319; pl. 27, fig. 2 [*partim*; not fig. 1, = *H. nodulosus* (Goldfuss); not figs 3–5, = *H. trecensis* Leymerie].
1874 *Holaster laevis* (Brongniart); Quenstedt: 620; pl. 86, figs 21–24.
non 1881 *Holaster laevis* Wright: 310; pl. 72, fig. 1 [= *H. nodulosus* (Goldfuss)].
1894 *Holaster laevis* (de Luc, *in* Brogniart); Lambert: 20; pl. 1, figs 1–3.
1917 *Holaster laevis* (de Luc); Lambert: 202.
1924 *Holaster laevis* (de Luc); Lambert & Thiéry: 404.
1955 *Holaster laevis* (de Luc Ms) Agassiz; Szörényi: 227; pl. 12, figs 4–7, 9.
1963 *Holaster laevis* (de Luc); Cayeux: 18; fig. 3.

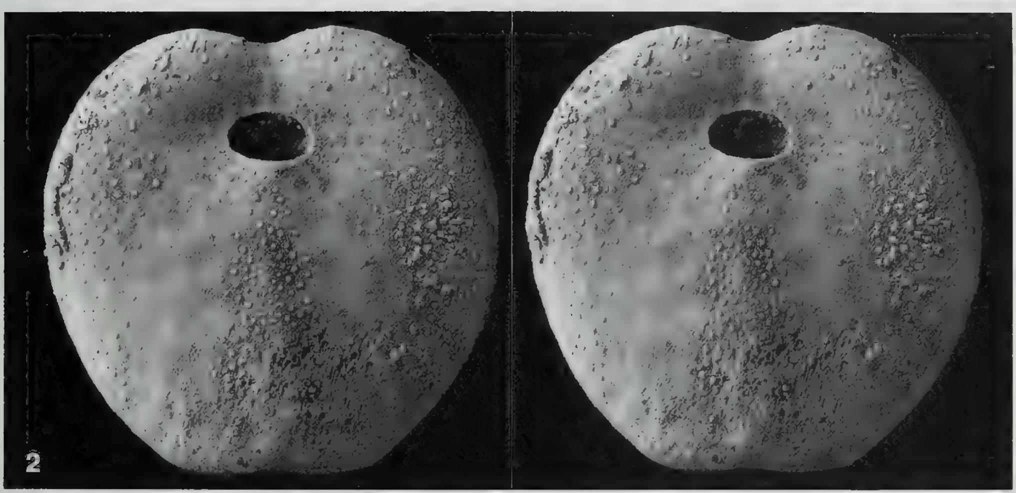
Material. Only a single specimen belonging to this species (E.80544) was collected at Wilmington and the following description is based on this.

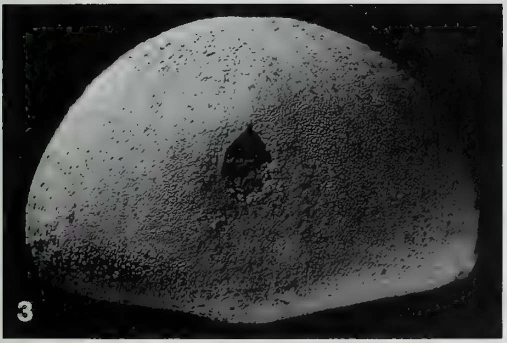
Stratigraphical occurrence and distribution. At Wilmington *H. laevis* was found at the base of the quarry, 1020 cm below standard datum level. Elsewhere in Britain the species is known from the Upper Greensand of Wiltshire.

Description. *SIZE AND SHAPE*. The Wilmington specimen is 24·4 mm in length and 24·8 mm in width (width 102% of the length). In outline the test is cordate with a small but definite anterior notch and a broad truncated posterior giving the test a rather squat appearance (Fig. 54a, b). The widest point on the test lies 47% of the test length from the anterior border. The anterior groove at the ambitus is a broad, uniformly U-shaped sulcus which at its deepest is 4% of the test length. Lateral carinae are not developed and the groove shallows and disappears adapically. On the oral surface, the region around the anterior border of the peristome is slightly sunken and the frontal groove is only feebly developed.

Test height is 66% of the length. The tallest point on the test coincides with the apical disc and lies 46% of the test length from the anterior border. In profile the base of the test is almost flat and the upper surface is uniformly vaulted and slopes steeply towards the anterior. At the anterior the ambitus lies more or less at the base and there is a sharp angle between the anterior and oral faces. The posterior is sharply truncated and is very slightly undercut below the upper rim of the periproct and slopes very slightly outwards below the periproct (Fig. 54a).







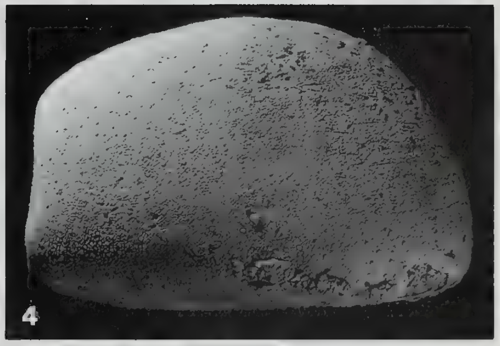


Plate 29

Holaster laevis (Brongniart)

Figs 1–4 E.80544: 1, apical; 2, oral; 3, posterior; 4, lateral, anterior to left. Basal part of the Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 2·5).

Viewed from the front, the base of the test is more or less flat except where the peristome projects down slightly, while the dorsal surface is uniformly vaulted. Here the ambitus occurs at about 20–30% of the test height above the base.

APICAL DISC. The apical disc lies at about mid-length and is relatively short and squat in comparison with those of other species of *Holaster*. The length of the apical disc is only 13% of the test length and at its broadest the width of the apical disc is 56% of its length. Apical disc plating is shown in Fig. 52a. The anterior ocular is short and squat. Ocular plates I and V are rather squarish in outline and obviously smaller than oculars II and IV. The madreporite (genital plate 2) is no larger than genital plates 1 and 4, and is covered in small hydropores. Genital plate 3 is noticeably smaller than the other genital plates, but remains in broad contact with ocular plate IV.

AMBULACRA. The paired ambulacra are lanceolate and sub-petaloid adapically whereas the anterior ambulacrum is non-petaloid. There are 26 ambulacral pores in the anterior ambulacrum at a test length of 24·4 mm. These are most closely spaced adapically and become gradually more widely spaced adorally. Ambulacral pores are minute isopores with a narrow interporal partition and a small neural canal. They are 0·3 mm in diameter and are set strongly oblique to the horizontal plate sutures. The interporal region of ambulacrum III is 2·1 mm in width at the ambitus.

The anterior paired ambulacra are very slightly curved. The two columns of pores are unequal, the anterior column of pores being approximately 50% of the width of the posterior adapically. These pores are conjugate isopores and there is a moderately broad interporal zone (Pl. 29, fig. 1). They are well developed adapically but become rapidly smaller, more widely spaced and circumflexed at about 60% of the distance to the ambitus. The base of the petaloid zone is indistinct. The isopores in the posterior column are 0·8 mm in width when fully developed. The posterior paired ambulacra are straight and lanceolate. The two columns of pores are equally developed and adapical pores are conjugate isopores 0·7 mm in width. The pores become smaller, more widely spaced and circumflexed at about 50% of the distance to the ambitus. The anterior paired ambulacra form an angle of 140° to the anterior while the posterior paired ambulacra form an angle of 75° to the posterior.

At the ambitus and over most of the oral surface the ambulacral pores are minute isopores. Larger isopores are found adjacent to the peristome. There are 2 phyllode pores per column in the anterior ambulacrum, 5 in ambulacra II and IV and 4 in ambulacra I and V.

INTERAMBULACRA. At the ambitus interambulacral zones are more than twice as broad as ambulacral zones. The anterior interambulacra are smoothly rounded without the slightest development of carina beside the anterior groove. The dorsal part of the posterior interambulacrum is weakly carinate above the periproct, beneath which there is a shallow depression.

On the oral surface the posterior interambulacrum is moderately broad and wedge-shaped (Fig. 55). The labral plate, which does not project over the peristome, is relatively small and only a little longer than it is broad. It is 12% of the test length, and its posterior border is more or less straight. Succeeding plates are arranged alternately and the plastron is meridosternous. There are a total of 16 plates per column in the posterior interambulacrum and the periproct is situated between plates 7a, 8b and 9a, 10b.

PERIPROCT. The periproct is teardrop-shaped in outline with a rounded adoral edge and a pointed adapical edge. The height of the periproct is 26% of the test height and its width is 57% of its height. The periproct lies at the top of the posterior face and the base of the periproct is 43% of the test height above the base of the test.

PERISTOME. The peristome is oval in outline. Its length is 11·5% of the test length and the width of the peristome is 1·6 times the length. The anterior edge of the peristome lies 21% of the test length from the anterior border. The peristome is rimmed by a feeble lip.

TUBERCULATION. Dorsal tuberculation is rather heterogeneous. In as far as it is preserved, plates in interambulacra 2 and 3 and in the anterior column of interambulacra 1 and 4 each have a larger primary tubercle and a sparse scattering of smaller secondary tubercles. The primary tubercles are larger adapically and towards the ambitus become smaller and more like

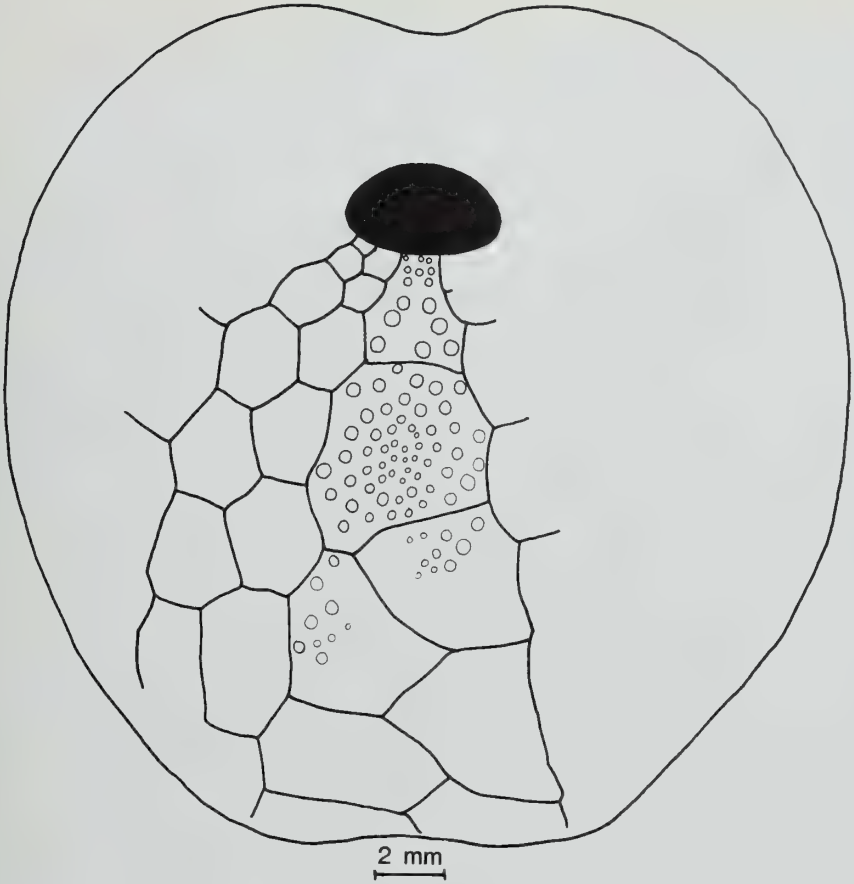


Fig. 55 Camera lucida drawing of the oral plating in *Holaster laevis* (E.80544) from the Lower Cenomanian of Wilmington.

the secondary tubercles. Primary tubercles are absent from the posterior column of plates of interambulacra 1 and 4 and from interambulacra 5, except possibly immediately adjacent to the apical disc. Miliary tubercles occur amongst the primary and secondary tubercles but are not particularly dense.

On the oral surface tubercles are densely packed on the plastron, without intervening miliaries, and continue up to the lip of the peristome. Those tubercles adjacent to the peristome are noticeably smaller and tubercles also decrease in size towards the growth centre of each plastron plate. There are broad tubercle-free tracts between the plastron and the region of lateroventral tubercles.

Remarks. This is a common and well-established species from the Albian of north-western Europe. Unfortunately it has often been confused with *H. nodulosus* (Goldfuss) and both Wright (1881) and Cotteau (1865) have figured specimens of *H. nodulosus* under the name *laevis*. The species name was coined by de Luc in an unpublished museum catalogue and was used by Brongniart (1822). Brongniart's figure is not particularly good and his description sketchy but an excellent figure of this species was given by Agassiz (1839), who is responsible for clearly establishing this species and distinguishing it from *H. nodulosus*. A full synonymy up to 1873 can be found in de Loriol (1873).

H. laevis differs from *H. nodulosus* in a number of characters. First of all in overall shape *H. laevis* is rather more squat and has a truncated posterior, whereas *H. nodulosus* is more elongate and tapers posteriorly to a rounded point (Fig. 54). The test is generally taller in *H. laevis* and its tallest point lies slightly anterior of mid-length, coinciding with the apical disc. In *H. nodulosus* the tallest point of the test lies a little posterior of the apical disc, which is itself slightly closer to the anterior border. The apical disc in *H. laevis* is much shorter and the paired ambulacra more convergent adapically than in *H. nodulosus*. The base of the test is flatter in *H. laevis* and there is a sharp angle between the base of the test and the backward sloping anterior, whereas in *H. nodulosus* the anterior face is more convex and the ambitus higher. Finally, in *H. laevis* the labrum is relatively short and the plastron widens considerably towards the posterior whereas in *H. nodulosus* the labrum is narrow and elongate and the plastron is parallel-sided towards the posterior.

Holaster bischoffi Renevier 1868
Pl. 30, figs 1–4; Figs 56–59

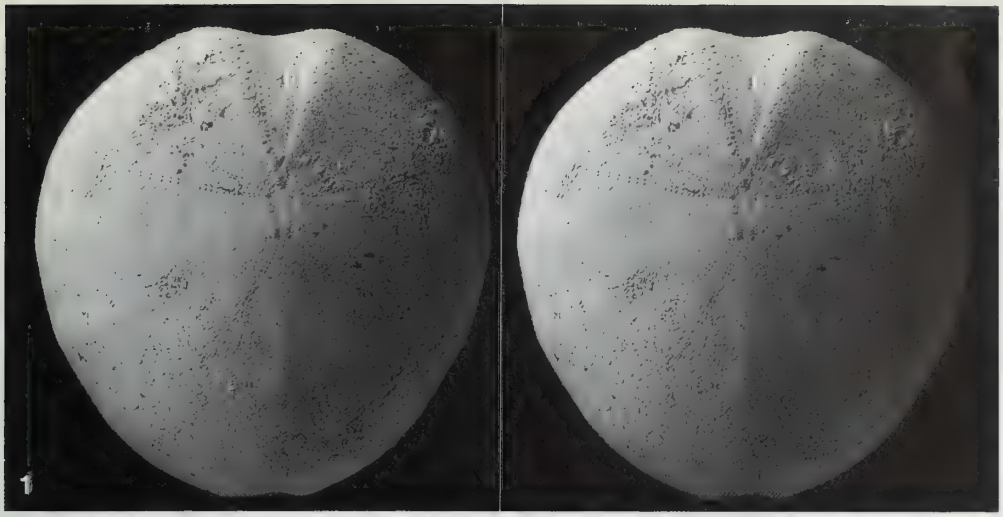
1868 *Holaster Bischoffi* Renevier: 446.
1873 *Holaster Bischoffi* Renevier; de Loriol: 333; pl. 28, figs 1, 2.
1874 *Holaster altus* Quenstedt: 620; pl. 86, fig. 25 (*non* Agassiz).
1898 *Holaster altus* Jukes-Browne: 246; pl. 24, figs 1–7 (*non* Agassiz).
non 1963 *Holaster bischoffi* Cayeux: 16; fig. 1 [= *H. altus* Agassiz].

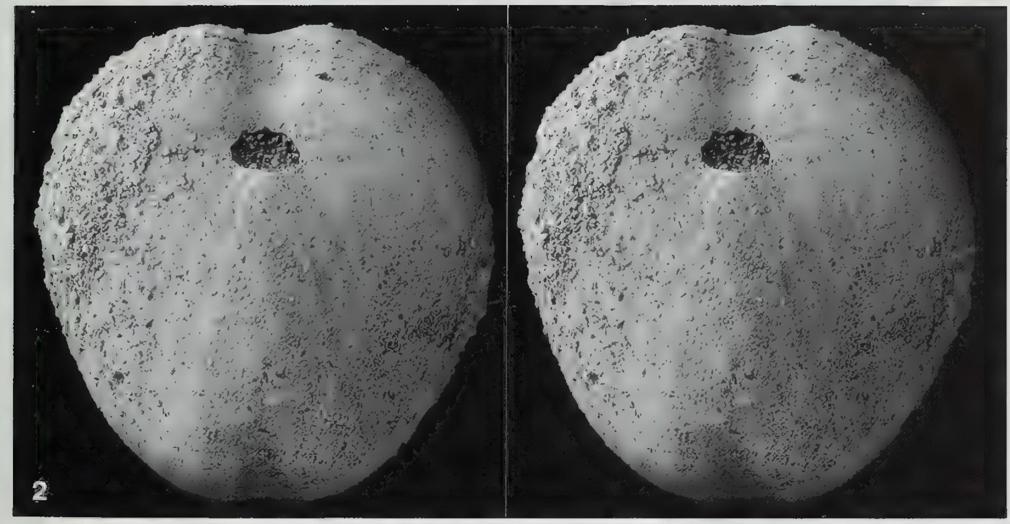
MATERIAL. This species is abundant at Wilmington and a large number of specimens were collected *in situ*. Fifty-two specimens (E.80229–83) were analysed biometrically.

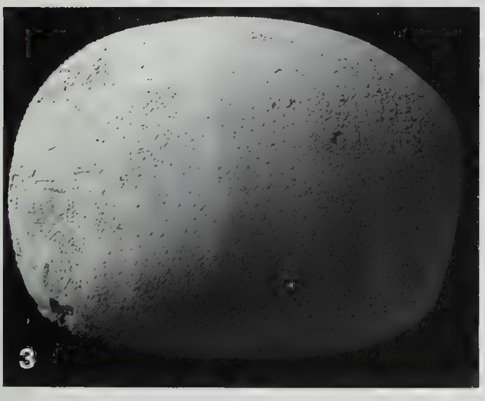
STRATIGRAPHICAL OCCURRENCE AND DISTRIBUTION. At Wilmington *H. bischoffi* is almost exclusively confined to the Grizzle (Fig. 7, pp. 18–19) and belongs to the Lower Cenomanian. With the exception of one small immature specimen collected 482 cm below standard datum, all the specimens came from between 85 and 235 cm below standard datum. Elsewhere in Britain this species occurs in beds of a similar age on the south Devon coast.

DESCRIPTION. *SHAPE AND SIZE*. The test is weakly cordate in outline and suboval in profile. The oral surface is uniformly and gently convex. Test length ranges from 14·5–36·5 mm (mean = 26 mm; SD = 5·9; N = 52) and test width from 13·5–36·3 mm (mean = 25 mm; SD = 4·9; N = 52). Test width is 86–97% of the test length (mean = 95%; SD = 2·5; N = 52). The widest point of the test is at 40–51% of the test length from the anterior of the test (mean = 45%; SD = 3·0; N = 52), which coincides more or less with the interradial suture of interambulacra 1 and 4 at the ambitus. Test height ranges from 11·5–26·2 mm (mean = 19·4 mm; SD = 3·4; N = 51) which is 67–88% of the test width (mean = 77%; SD = 4·4; N = 51) and 63–80% of the test length (mean = 73%; SD = 3·4; N = 51). The tallest point of the test lies between 62 and 95% of the test length from the anterior border (mean = 77%; SD = 8·4; N = 51). The test in outline tapers posteriorly almost to a point and the periproct is hidden from view from above. The anterior groove is broad and shallow and very weakly developed even at the ambitus. At the ambitus, the anterior groove is 0·8–3·2% of the test length in depth (mean = 2%; SD = 0·6; N = 51) and 21–32% of the test width in breadth (mean = 26%; SD = 2·2; N = 52). The frontal groove continues adorally to the peristome but is very shallow, while adapically it becomes almost flush with the surrounding test. In profile the base, anterior and apical surface are all gently convex. The posterior is truncated and is slightly undercut (Pl. 30, fig. 3). The periproct lies at the top of this truncated region. In frontal view, the dorsal and ventral surfaces are both uniformly convex, although the dorsal surface is only weakly convex. The ambitus lies approximately $\frac{1}{3}$ of the test height above the base.

APICAL DISC. The apical disc is elongate and in length is 16–22% of the test length (mean = 18%; SD = 2·0; N = 46). The anterior edge of the apical disc lies 28–40% of the test length from the anterior border of the test (mean = 32%; SD = 2·4; N = 47). The apical disc thus lies slightly anterior of the mid-point so that the posterior edge of the apical disc more or less coincides with the mid-length of the test. The width of the apical disc is 28–42% of its







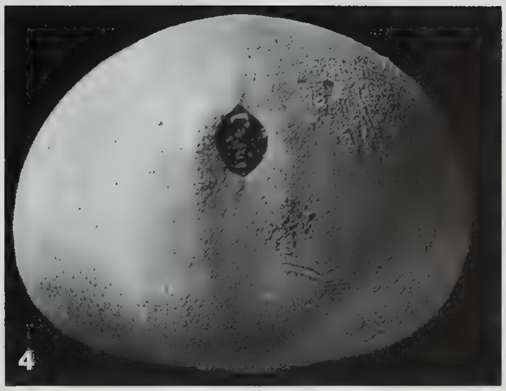


Plate 30
Holaster bischoffi Renevier
Figs 1, 3, 4 E.80223: 1, apical; 3, lateral, anterior to left; 4, posterior. Upper part of the Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 2).
Fig. 2 E.80242: oral. As last (× 2).

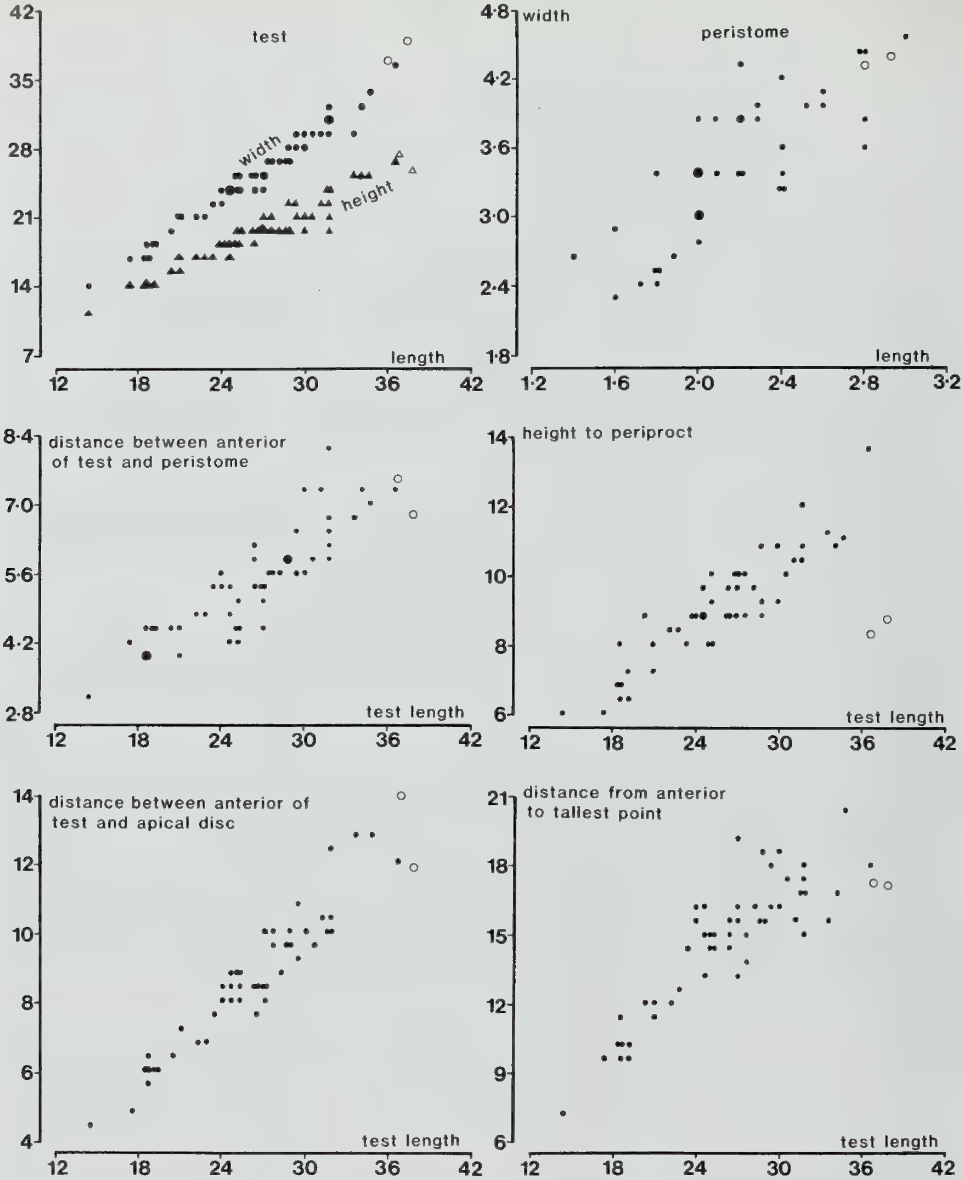


Fig. 56 Biometric data on *Holaster bischoffi* (●, ▲) and *H. subglobosus* (○, △).

length (mean = 34%; SD = 3·8; N = 43). Ocular III is angular and projects forwards (Fig. 58). Genital plate 2 (the madreporite) is moderately large and much of its surface is covered in hydropores. Genital plate 3, in contrast, is greatly reduced and is only a little larger than the gonopore it bears. Its contact with ocular plate IV is extremely small and in a few specimens the two do not touch. Ocular plates IV and II are noticeably larger than the other oculars and abut along the midline. Genital plates 1 and 4 are equally developed and similar in size to the madreporite. In about 60% of individuals, genital plate 1 lies slightly more posterior than genital plate 4, the reverse being true in the remaining 40%. The posterior ocular plates are elongate.

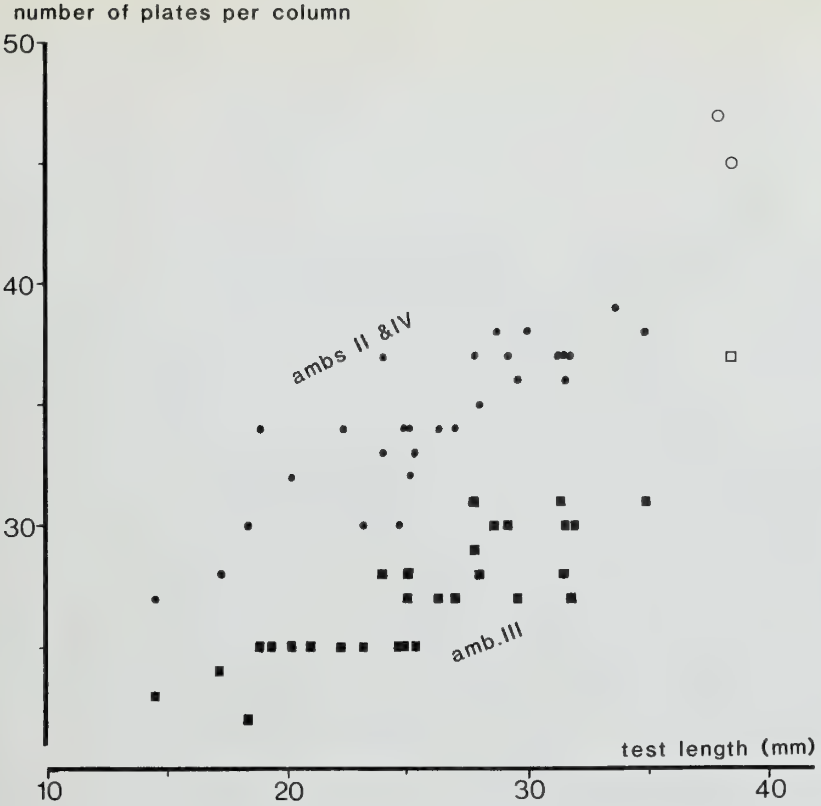


Fig. 57 Number of ambulacral plates plotted against test size for *Holaster bischoffi* (●, ■) and *H. subglobosus* (○, □).

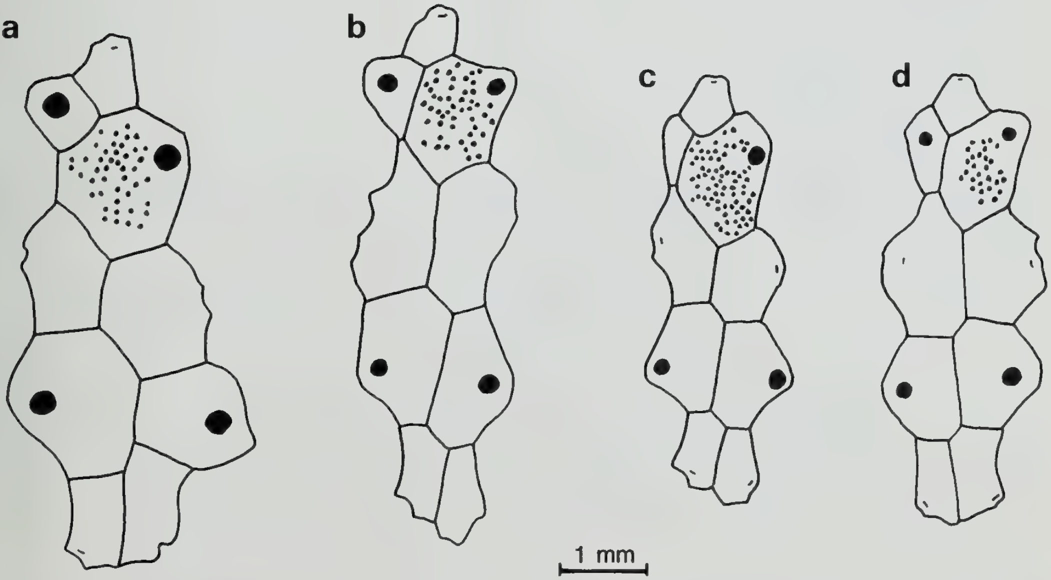


Fig. 58 Camera lucida drawings of apical disc plating in *Holaster bischoffi* from the Lower Cenomanian of Wilmington: a, E.80241; b, E.80242; c, E.80200; d, E.80202.

AMBULACRA. Ambulacrum III lies in a weak sulcus. All ambulacral pores are minute isopores orientated obliquely. These are densely packed adapically and become progressively more widely spaced and even smaller adambitally (Pl. 30, fig. 1). They lie near the adradial suture and occupy only a small portion of each plate. The lowest three pores in each column are noticeably larger and have a prominent interporal ridge and an oval periporal rim (Pl. 30, fig. 2). At a test diameter of about 15 mm there are 23 plates in each column of ambulacrum III, rising to between 28 and 33 by 25–35 mm.

The lateral and posterior paired ambulacra are all very similar and are non-petaloid. Ambulacral pores are most closely packed adapically and becomes progressively more widely spaced adambitally. The dorsal pores are relatively small isopores (Pl. 30, fig. 1) lacking any identifiable attachment rim. The pore pairs are oval and weakly circumflexed and there is no recognizable neural canal. The interporal partition is narrow and flush with the test surface. Except for the two or three pores immediately adjacent to the apical disc, adapical pores are moderately well developed and become progressively smaller adambitally. Near the ambitus the isopores are extremely small and difficult to locate. Here they are set obliquely. Adorally the isopores remain minute except immediately adjacent to the peristome where there are three larger phyllode pores per column. In the paired anterior ambulacra there are 27 plates per column at a test length of 15 mm, which rises to 35–38 plates at a test length of 30–35 mm (Fig. 56). The posterior paired ambulacra have a similar number of plates at all sizes.

INTERAMBULACRA. The interambulacra are composed of relatively large, broad plates. On the oral surface the plastron is meridosternous and is composed of a small, rather elongate labral plate followed by large alternating triangular plates (Fig. 59), three in each column. The plastron is narrow and only measures 26–38% of the test width at its broadest (mean = 32%; SD = 1·5; N = 42). In the posterior interambulacrum there are 15 plates per column at a test length of 17 mm, rising to 17 or 18 plates at a test length of 25–35 mm. The most proximal plate in the other interambulacra is a single triangular plate which borders the peristome (Fig. 59).

PERIPROCT. The periproct lies relatively high on the posterior surface. It is lensoidal in outline, pointed both adapically and adorally. Its height is 2·6–5·6 mm (mean = 3·8 mm; SD = 0·6; N = 46), which is 18–24% of the test height (mean = 20%; SD = 1·4; N = 45). The breadth of the periproct is 57–84% of its height (mean = 70%; SD = 6·0; N = 43). The periproct lies a little above mid-height, at the top of the truncated posterior surface. The base of the periproct lies at 39–56% of the test height above the base of the test (mean = 48%; SD = 3·6; N = 48). A pair of weak carinae run vertically down from either side of the periproct with a small, slightly concave, tubercle-free zone in between, directly beneath the periproct. The periproct lies between plates 7a, 8b and 9a, 10b in all specimens.

PERISTOME. This is small and roughly oval in outline. The anterior border of the peristome is generally more convex than the posterior border, which is almost straight. The labral plate does not overhang the peristome which therefore faces directly down. The length of the peristome is 6–10% of the test length (mean = 8%; SD = 0·3; N = 42). The anterior border of the peristome lies 16–24% of the test length from the anterior border of the test (mean = 20%; SD = 2·0; N = 51).

TUBERCULATION. Tubercles over the aboral surface are minute and superficially the test looks tubercle-free. Dorsal tubercles have a boss slightly less than 0·2 mm in diameter and an areole about 0·25 mm in diameter. These tubercles are perforate and crenulate and are moderately well scattered. Miliary tubercles are well developed in between the primary tubercles. Tubercles become slightly larger towards the anterior border and those at the outer edges of the frontal groove are about twice the diameter of other dorsal tubercles. On the oral surface tubercles are densely packed on the plastron and extend over the labrum up to the border of the peristome. Lateroventral tubercles are less densely packed and there are interspersed miliary tubercles. Areole enlargement is not marked in any of the oral tubercles.

REMARKS. *Holaster bischoffi* was first described by Renevier (1868) and first figured by de Loriol (1873). In Britain this species was confused with *H. altus* (which, in my opinion, is a distorted specimen of *H. subglobosus*) and this name was used by Jukes-Browne (1898) for *H. bischoffi* from Wilmington.

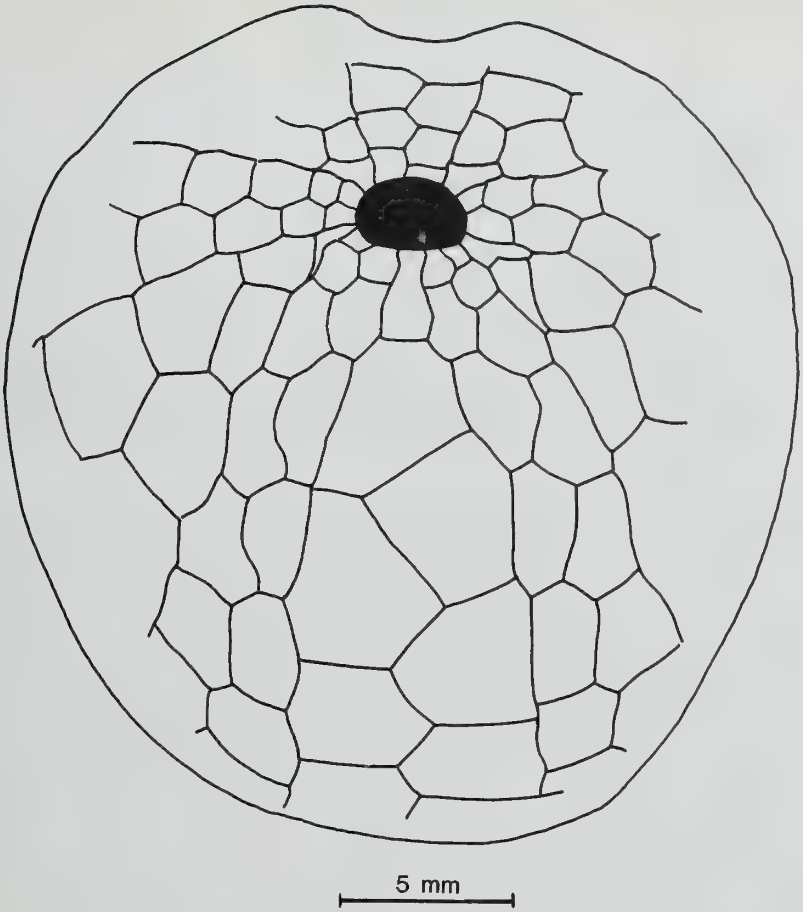


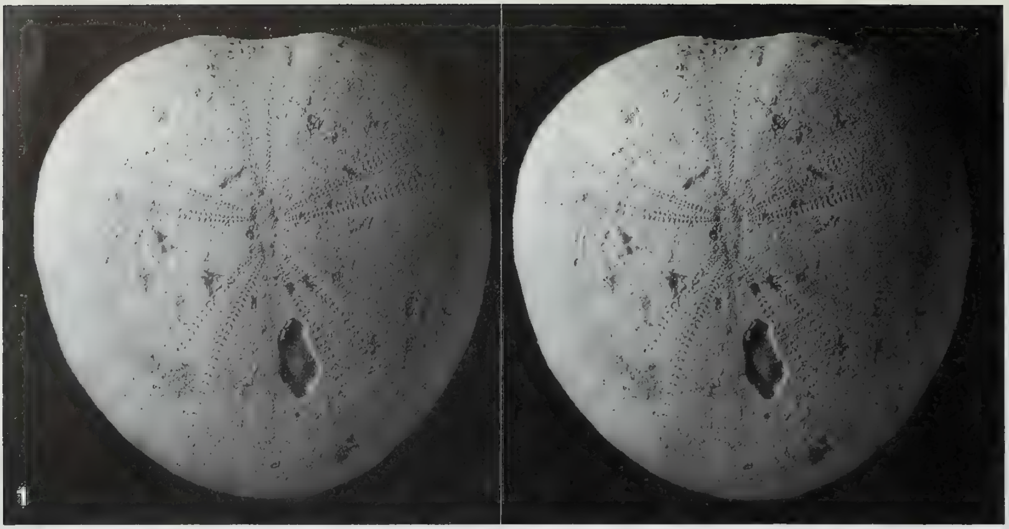
Fig. 59 Camera lucida drawing of oral plating in *Holaster bischoffi* (E.80208) from the Lower Cenomanian of Wilmington.

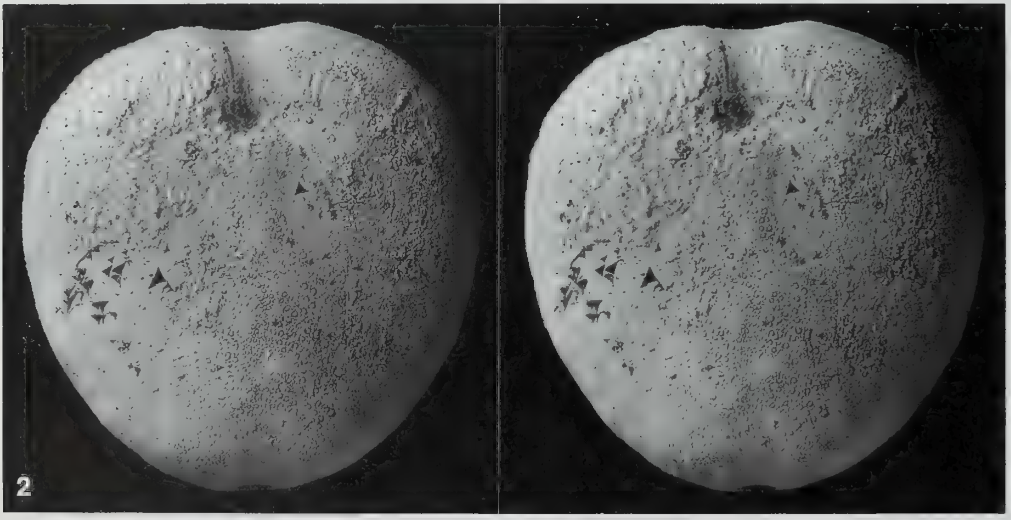
This species differs from *H. subglobosus* in a number of respects and the two cannot be confused when seen side by side. *H. bischoffi* differs from similar-sized *H. subglobosus* in having fewer ambulacral plates per column (Fig. 57), a more rectangular profile with the anterior more vertical and less convex and the dorsal surface more flat, and the periproct situated proportionally higher on the posterior surface (Fig. 56, and compare Pls 30 & 31). In the apical disc of *H. bischoffi* ocular IV and genital 3 barely touch (Fig. 58), whereas in *H. subglobosus* these two plates have a considerably broader contact (Fig. 60).

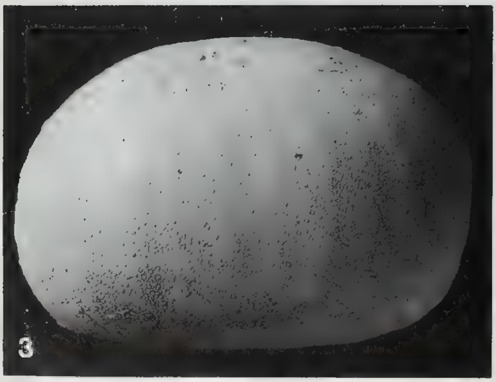
Holaster subglobosus (Leske 1778)

Pl. 31, figs 1–4; Pl. 40, fig. 1; Figs 56, 57, 60a, b, 61

1778 *Spatangus subglobsus* Leske: 240; pl. 54, figs 2, 3.
1881 *Holaster subglobosus* (Leske) Wright: 319; pl. 73, fig. 1 (see also for full synonymy).
1883 *Holaster altus* Bucaille: 21; pl. 5, figs 1–8 (*non* Agassiz).
1894 *Holaster subglobosus* (Leske); Lambert: 61.
1917 *Holaster subglobosus* (Leske); Lambert: 205.
1924 *Holaster subglobosus* (Leske); Lambert & Thiéry: 403.
1955 *Holaster subglobosus* (Leske); Szörényi: 225; pl. 12, figs 1–3; pl. 13, fig. 2.
1963 *Holaster subglobosus* (Leske); Cayeux: 21; fig. 6.
1972 *Holaster subglobosus* (Leske); Ernst: 117; fig. 20, 9.


1


2


3

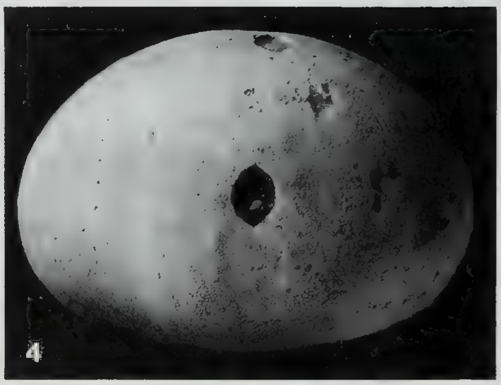

4

Plate 31
Holaster subglobosus (Leske)
Figs 1–4 E.80284: 1, apical; 2, oral; 3, lateral, anterior to left; 4, posterior. Middle Cenomanian, White Hart sand pit, Wilmington, Devon (× 1·8).

MATERIAL. Only two specimens (E.80284 and E.80620) of this species were collected at Wilmington, so for comparison the relatively abundant material from the Middle Cenomanian Bed B of the south Devon section was also examined, together with a similar-sized individual (E.16920) from the Grey Chalk of Folkestone, Kent.

STRATIGRAPHICAL OCCURRENCE AND DISTRIBUTION. Both specimens from Wilmington came from loose blocks of Wilmington Limestone and thus are from the Middle Cenomian. It is a relatively common species at this level in south Devon, Dorset, Kent and Norfolk.

DESCRIPTION. *SHAPE AND SIZE.* Although this species can grow to a considerable size, commonly reaching 8 cm in length, those from Wilmington are only half this size. In outline the test is oval and faintly cordate. The best preserved specimen from Wilmington (E.80284) has a length of 37·0 mm and a breadth of 35·4 mm (98% of the test length). Test height is 25·4 mm (68% of the test length) and the tallest point of the test coincides with the apical disc and lies 46% of the test length from the anterior border of the test. The widest point on the test lies 43% of the test length from the anterior border. There is a very feeble frontal groove which is only slightly concave. At its deepest it is only 1·0–1·5% of the test length and at its broadest, about 25% of the test width; adapically it becomes imperceptible. In outline the posterior part of the test is uniformly rounded.

In profile the aboral surface is gently convex and curves uniformly and gradually around the anterior. The posterior surface is slightly convex and the most posterior point of the test is at the adapical edge of the periproct. Beneath this, the test slopes inwards very slightly and is almost, but not quite, straight. From the anterior, the dorsal surface appears broad and gently convex.

APICAL DISC. The apical disc is elongate, with a length 14–18% of the test length and a width 41–44% of its length. The anterior edge of the apical disc lies 32–37% of the test length from the anterior border of the test and the whole disc lies slightly anterior of mid-length. The plating arrangement is shown in Fig. 60a, b. Genital plate 3 is smaller than the other genital

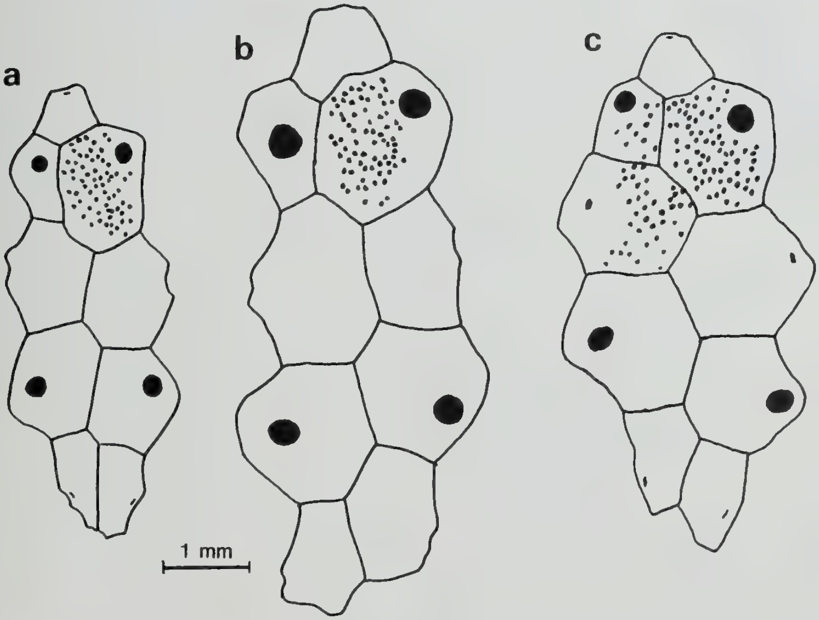


Fig. 60 Camera lucida drawings of apical disc plating in: a, b, *Holaster subglobosus;* a, E.80284, Wilmington Limestone, Middle Cenomanian, and b, E.16780, Grey Chalk (Cenomanian) of Folkestone. c, *Holaster revestensis*, E.80624; 'Lower Greensand', basal Cenomanian, White Hart pit, Wilmington, Devon.

plates, but remains broadly in contact with ocular plate IV. Ocular plate III is rather small and squat while ocular plates I and V are rather elongate. Genital plate 4 is as large as the madreporite.

AMBULACRA. The anterior ambulacrum is almost flush with the test adapically and becomes slightly depressed adorally. Its ambulacral pores are small isopores, 0·4 mm in diameter, slightly oblique to the horizontal suture and with a low interporal partition. They are most densely packed adapically and become progressively more widely spaced adambitally. Except for the adoral phyllode pores, all pores in the frontal ambulacrum are identical.

The paired ambulacra are non-petaloid and lanceolate, and are flush with the surrounding interambulacra. Dorsal pores are isopores which are very slightly circumflexed. Except for the most adapical two or three isopores, the pores remain uniform in size for about 70% of the distance to the ambitus, beyond which they decrease in size rapidly and become more oblique. In ambulacra II and IV at a test length of 38 mm the two columns of pores are unequal; in the posterior column the isopores are 0·8 mm in width whereas in the anterior column they are 0·6 mm. In ambulacra I and V the two columns of ispores are similar in size and measure 0·6 mm in width. At this size there are 37 plates in each column of the anterior ambulacrum and 45–47 plates in the other ambulacra.

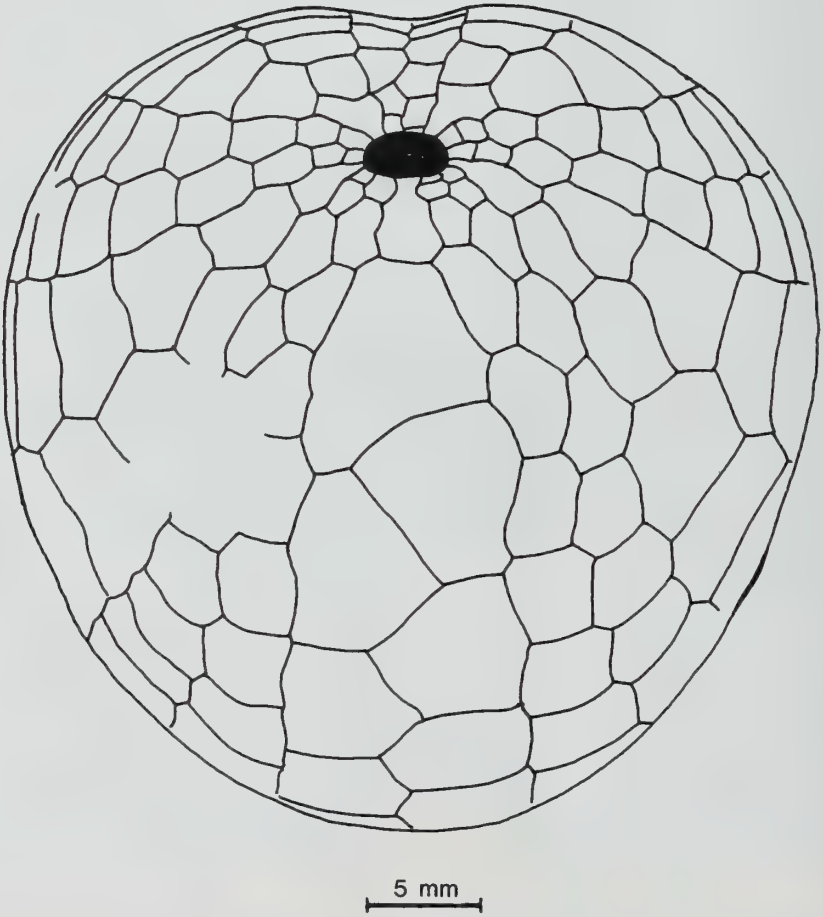


Fig. 61 Camera lucida drawing of the oral plating in *Holaster subglobosus* (E.16920) from the Grey Chalk (Cenomanian) of Folkestone, Kent.

Ambital and adoral pores are generally small and insignificant isopores, but immediately adjacent to the peristome there are large phyllode pores. These are circular isopores with a prominent bulbous interporal partition. There are three such phyllode pores in each ambulacral column.

INTERAMBULACRA. Interambulacral zones are about $1\frac{1}{2}$ times the width of ambulacra at the ambitus. Adorally each interambulacrum ends as a single triangular plate which borders onto the peristome (Fig. 61). The labral plate is relatively small and rather elongate, with an almost straight posterior border. Subsequent plates on the plastron are triangular in outline and arranged alternately. The plastron extends posteriorly as far as plates 4a, 4b and there are a total of 18 plates in interambulacrum 5 at a test length of 38 mm. The plastron is absolutely flush with the rest of the test and is not keeled or nodate. The junction between the posterior end of the plastron and the adoral part of the posterior surface is gradual and curved. There are no interambulacral carinae bordering the frontal groove either.

PERIPROCT. The periproct is oval in outline and comes to a weak point both adapically and adorally. It is relatively small, only 19% of the test height, and variable in width (width is 58% and 69% of the height in the specimens examined). The periproct lies between plates 7a, 8b and 9a, 10b. It is situated at about mid-test height and the base of the periproct lies 32–33% of the test height above the base of the test.

PERISTOME. This is oval in outline with a convex posterior border. There is no lip to the peristome or surrounding rim and the peristome is not sunken. It is 7–8% of the test length in length and the width of the peristome is 1·5 times the length. The anterior edge of the peristome lies 18–20% of the test length from the anterior border of the test.

TUBERCULATION. Tuberculation over the aboral surface is uniform and fine. The primary tubercles are minute and are surrounded and separated by numerous miliary tubercles. Tubercles are hardly any larger on the anterior face of the test and, as distinct from most of the other species of *Holaster*, there are no larger tubercles bordering the anterior ambulacrum. On the plastron tubercles are relatively densely packed and continue right up to the peristome. Two distinct centres of tuberculation are present in the subanal region. Lateroventral tubercles are moderately widely spaced and there are scattered miliary tubercles in this region.

REMARKS. This well known species is common in the Middle Cenomanian of north-west Europe. Its occurrence in Britain was firmly established by Forbes (1852), who provided excellent description and figures. It differs from the closely related *H. bischoffi* in its more rounded overall shape, the proportionally lower position of the periproct and the greater number of ambulacral plates at a given size (see p. 151 and Figs 56 & 57).

Holaster revestensis Lambert 1924

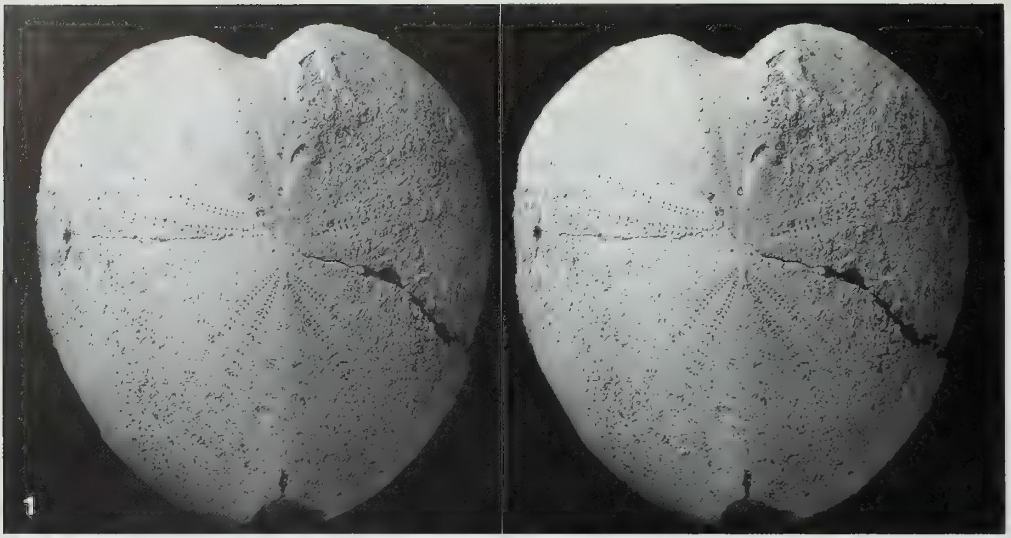
Pl. 35, fig. 1; Fig. 60c

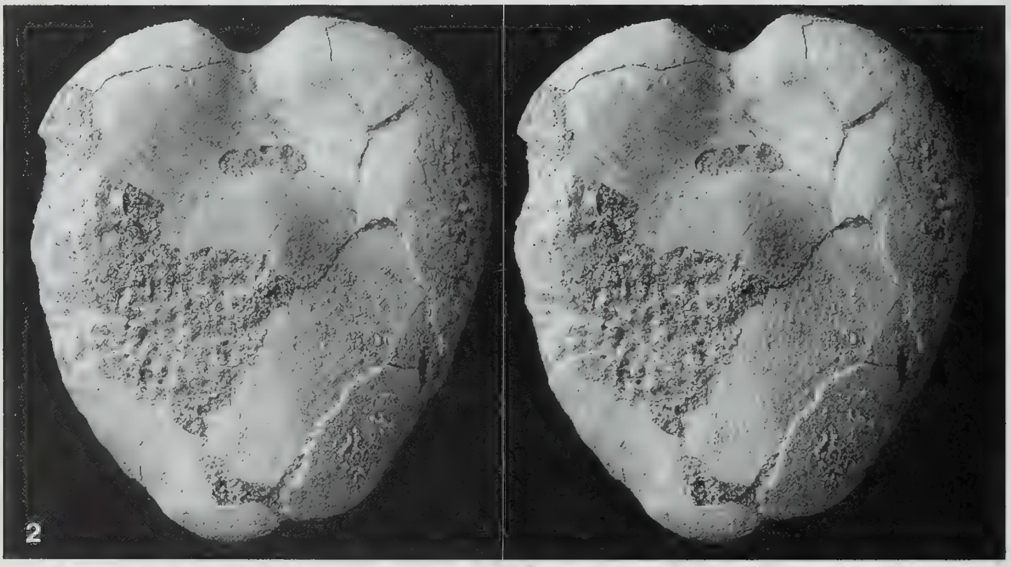
1917 *Holaster revestensis* Lambert: 210 [*nomen nudum*].
1924 *Holaster revestensis* Lambert, *in* Lambert & Thiéry: 404; pl. 10, figs 9, 10.

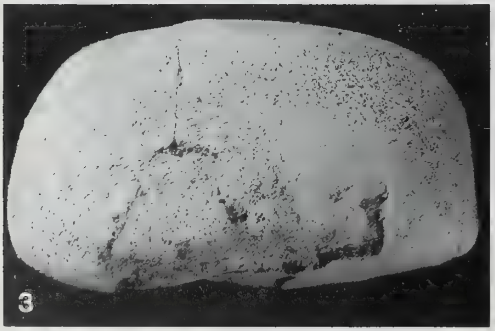
MATERIAL. A single specimen (E.80624) of this distinctive species was collected at Wilmington, but unfortunately it is damaged and a full description cannot be given.

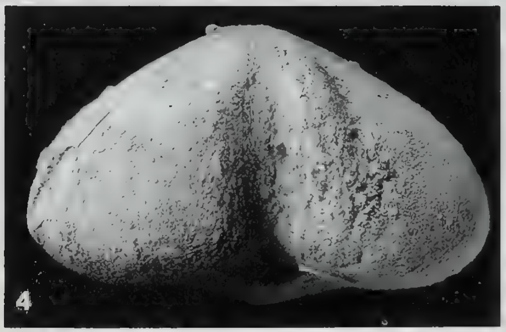
STRATIGRAPHICAL OCCURRENCE. The Wilmington specimen came from the Upper Greensand, 962 cm below the standard datum level. It therefore comes from beds low in the Lower Cenomanian. This species has not previously been reported from Britain.

DESCRIPTION. *SIZE AND SHAPE.* The test is broad, flat and ovoid in outline with a small shallow frontal groove. The posterior has been damaged, but by estimation the length of the test is approximately 33–34 mm. It is apparently slightly longer than broad, with a breadth approximately 94% of the length. The widest point on the test lies a little posterior of the anterior paired ambulacra, about 45% of the test length from the anterior border. The height of the test is approximately 50% of the length. The dorsal surface is broad and gently convex, with the tallest point on the test coinciding with the posterior portion of the apical disc. In profile the test is low, slightly convex dorsally and rounded anteriorly. The ambitus lies a little


1


2


3


4

below mid-height. The frontal groove is 9·5 mm broad at the ambitus (30% of the maximum test width) and 1·6 mm in depth (about 5% of the test length). The groove continues right to the apex but adapically it becomes progressively more shallow. It also continues adorally up to the peristome.

APICAL DISC. The apical disc is twice as long as it is broad and tapers both anteriorly and posteriorly (Fig. 60c, p. 153). It is 5·8 mm in length (approximately 17% of the test length) and the anterior edge of the disc lies at about 42% of the test length from the anterior border. The plates of the apical disc are arranged alternately rather than opposite. Ocular III is small and protrudes anteriorly. Genital plate 3 is small and squarish with broad contact zones with ocular plate IV and genital plate 2. The posterior two ocular plates are elongate and taper posteriorly. Hydropores perforate almost the entire surface of genital plate 2 and are also found over much of genital plate 3 and ocular plate IV. The gonopores are large and the posterior two are offset.

AMBULACRA. In this specimen only the dorsal portion of ambulacra can be examined. The paired ambulacra are flush with the test surface and the ambulacral pores, which are elongate conjugate isopores, are well developed. The two pores in each isopore taper towards each other and are linked by a sharp groove bounded adapically and adorally by a rim. In the anterior paired ambulacra the isopores in the anterior column are, at their widest, 1·1 mm in breadth and are 80% of the width of those in the posterior column, which are 1·4 mm at their broadest. The pore zones form a large part of the width of the ambulacra and the interporal perradial zone measures 1·6 mm at its broadest, which is only slightly larger than one of the pore zones. The isopores in the posterior paired ambulacra are similar to those of the anterior paired ambulacra except that both columns of pores are equally developed. The isopores in all four ambulacra are rather closely packed and broad conjugate pores continue for about 90% of the radial length to the ambitus. In the anterior paired ambulacra there are 31 pores per column to the ambitus, of which all but the three most adambital are broad conjugate isopores. The anterior paired ambulacra form an angle of 130° to the anterior, while the posterior paired ambulacra form an angle of 70° to the posterior.

Ambulacrum III is lightly sunken for its entire length. The ambulacral pores are small and difficult to see. They are isopores with a small circular attachment rim, obvious neural canal and a narrow interporal partition. These are about 0·3 mm in diameter and are highly inclined to the adoral suture of the plate. They are closely packed adapically but become more widely spaced adambitally.

INTERAMBULACRA. There is no dorsal carina. Plastron plating is not visible.

PERISTOME & PERIPROCT. Not visible.

TUBERCULATION. Most of the dorsal surface is covered in moderately densely packed and uniformly sized tubercles, 0·3 mm in diameter, with numerous interspersed miliary tubercles. Single rows of miliary tubercles separate successive isopores in the paired ambulacra. Bordering the frontal groove there are two highly irregular rows of noticeably larger tubercles 0·5–0·6 mm in diameter which stand out clearly. Within the frontal groove there are a couple of small primary tubercles close to each ambulacral pore while the rest of the groove is covered in miliary tubercles.

REMARKS. The name *Holaster revestensis* was first proposed by Lambert (1917) for an individual from the Cenomanian of Escragnolles but with no accompanying description or illustration. The name was validated in Lambert & Thiéry (1924) when Lambert gave a diagnosis and figure of the species. The overall flattened ovoid shape, the highly developed and extensive petals and the distinctive larger tubercles bordering the frontal groove make *H. revestensis* unlike any other British species.

Plate 32

Labrotaxis tricarinata (Lambert)

Figs 1, 3 E.80814: 1, apical; 3, lateral, anterior to left. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 1·8).

Fig. 2 E.80186, oral. As last (× 1·3).

Fig. 4 E.80185, anterior. As last (× 1·3). See also Pl. 33, fig. 3.

Genus *LABROTAXIS* Casey, 1960

Labrotaxis cenomanensis (d'Orbigny 1855)
Pl. 33, figs 1–2; Pl. 34, figs 1–4; Fig. 62

1840*b* *Holaster carinatus* Agassiz: 1 (*partim*) (*non* Lamarck).
1855 *Holaster cenomanensis* d'Orbigny: III; pl. 819, figs 7–12.
1873 *Holaster cenomanensis* d'Orbigny; Quenstedt: 621; pl. 81, figs 30, 31.
1917 *Holaster cenomanensis* d'Orbigny; Lambert: 207.
1924 *Holaster cenomanensis* d'Orbigny; Lambert & Thiéry: 403.

MATERIAL. Three specimens of this species were collected at Wilmington (E.80538, E.80621–3), of which only one was *in situ*. The following description is based on these three specimens.

STRATIGRAPHICAL OCCURRENCE AND DISTRIBUTION. At Wilmington the only specimen collected *in situ* came from 942 cm below standard datum, from the Lower Cenomanian. A second specimen is preserved in an identical lithology and almost certainly came from the same horizon. The third specimen is preserved rather differently, in a different lithology. This species has not previously been reported from Britain.

DESCRIPTION. *SIZE AND SHAPE*. The three specimens are 12·1, 19·4 and 24·5 mm in length and cordiform in outline. In the smallest specimen the test is longer than wide (test width = 88% of length) but in the larger specimens test width and test length are approximately equal. The widest point on the test lies slightly anterior (at 42% of the test length from the anterior border) in the smallest specimen but lies more or less centrally (49% of the test length from the anterior border) in the two larger specimens. Test height is 68–74% of test length (mean = 74%; SD = 3·0; N = 3) and the tallest point on the test lies at about mid-length in the two larger specimens (51% and 52% of the test length from the anterior border of the test). The frontal groove is well developed and continues right to the apex, although it has not yet appeared in the smallest specimen. At the ambitus the frontal groove has a depth of 5% of the total length of the test. Moderately well developed carinae border the frontal groove.

In profile the upper surface curves continuously from the mid-line to the anterior. The posterior is abruptly truncated and more or less vertical. The oral surface bulges downwards towards the posterior, giving the test a very characteristic profile. Viewed from the anterior, the dorsal surface slopes moderately steeply away from the mid-line and the plastron bulges downwards as a keel.

APICAL DISC. This is elongate and in length is 17% or 18% of the test length. The widest point on the apical disc is 35% or 40% of the length of the apical disc. The anterior edge of the apical disc lies 36% and 41% of the test length from the anterior border of the test. Ocular plate III is fairly equidimensional in outline. Genital plate 3 is smaller than the other genital plates and makes relatively broad contact with ocular plate IV. Ocular plates IV and II are the largest plates in the apical system. Ocular plates I and V are relatively elongate. Genital pores are not present in the 12·1 mm specimen and are relatively small and insignificant in the 19·4 mm specimen: these are both juveniles.

AMBULACRA. The ambulacra are non-petaloid and ambulacrum III is differentiated from the other ambulacra. The frontal ambulacrum is sunken from the apex to the peristome. Ambulacral pores, which are difficult to see without magnification, are minute oblique isopores approximately 0·2 mm in length. They are relatively widely spaced (except adapically) and leave

---

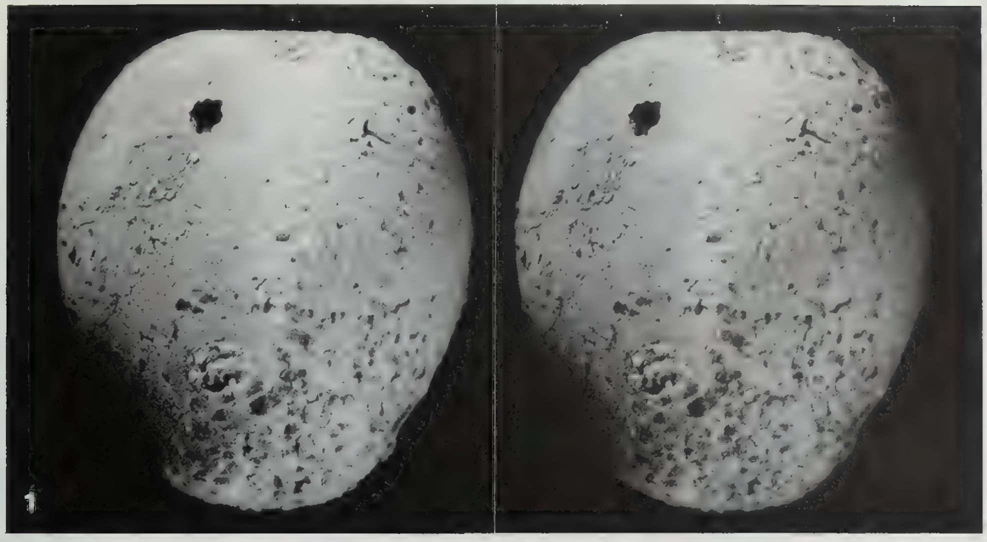
Plate 33

Labrotaxis cenomanensis (d'Orbigny), juvenile

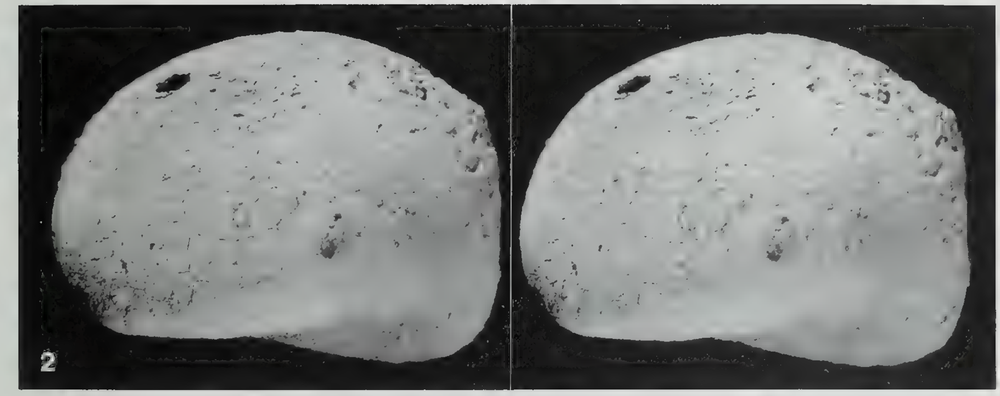
Figs 1, 2 E.80622: 1, apical; 2, lateral. Basal part of the Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 5·5).

Labrotaxis tricarinata (Lambert)

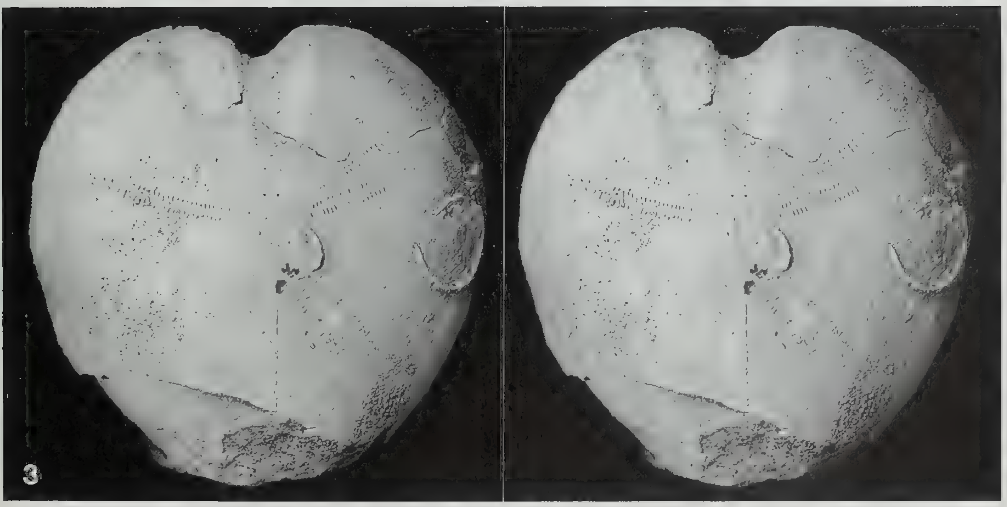
Fig. 3 E.80185, apical. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 1·2). See also Pl. 32, fig. 4.



1



2



3

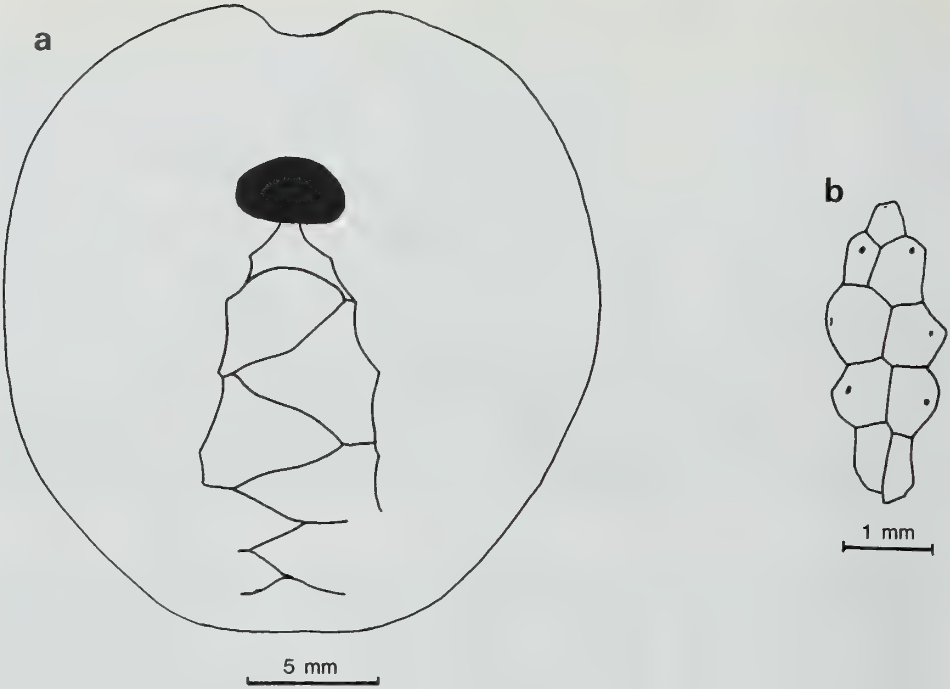


Fig. 62 Cameral lucida drawings of the oral plating in *Labrotaxis cenomanensis*: a, oral surface, E.80623; b, apical disc, E.80621.

a broad perradial tuberculate tract. The pores continue undifferentiated from the apex to close to the peristome where 2 or 3 phyllode pores are found.

Adapical pores in the anterior paired ambulacra are unequally developed in the two columns. The anterior column has small circumflexed isopores 0·3 mm in width, little larger than the pores of the frontal ambulacra. The posterior column has larger circumflexed isopores, 0·5 mm in width, with a relatively narrow interporal partition. Adambitally the pores become progressively further apart and also become smaller. At the ambitus and subambitally the pores are minuscule and very difficult to find. The posterior paired ambulacra have equally developed columns of pores. These are small circumflexed isopores, 0·5 mm in width, identical to those of the posterior column of the anterior paired ambulacra. Ambulacral pores are minute in the smallest specimen and invisible to the naked eye.

INTERAMBULACRA. These are moderately broad. The anterior interambulacra are developed into moderately sharp carinae which extend from the ambitus to the apical disc. There is also a weak carina posterior to the apical disc running to the periproct. The posterior interambulacrum on the oral surface is fairly broad and tapers rapidly near the peristome. The labral plate is broad and triangular (Fig. 62), with a concave posterior border. It is in contact with both of the succeeding plastronal plates, though it only just touches the left-hand side plate. Succeeding plastronal plates are triangular and alternate. There are, in addition to the labral plate, four plates per column to the posterior of the oral surface.

PERISTOME. The peristome is oval, being wider than long, and has a slightly convex posterior border (Pl. 34, fig. 2). The length of the peristome is 12% of the test length in the smallest specimen but only 10% of the test length in the two larger specimens. The peristome width is rather variable and is 1·3–1·7 times the peristome length (mean = 1·5; SD = 0·3; N = 3). The peristome is slightly sunken around the anterior border and the anterior edge of the peristome lies at 25% of the test length from the anterior border of the test at all sizes.

PERIPROCT. The periproct is relatively large and is lensoidal in outline. It is taller than broad and tapers to a point both adapically and adorally. The periproct lies high on the posterior face and cannot be seen from above or below. It has a height 28–33% of the test height and a width 68% of its height at 19·4 mm test diameter. In the smallest individual the periproct is more equidimensional in outline, its width being 84% of its height. The base of the periproct lies at 37–44% of the test height above the base of the test.

TUBERCULATION. Dorsal tubercles are minute and moderately dense with scattered miliary tubercles in between. Two irregular rows of larger and more closely spaced tubercles line the margins of the frontal groove. On the oral surface the posterior interambulacrum has a moderately dense covering of tubercles extending to the peristome. The periplastronal zones are free of tubercles, and tubercles in the lateroventral zones are more scattered than those on the plastron with a small number of interspersed miliary tubercles.

REMARKS. This species was erected in 1855 by d'Orbigny on a juvenile specimen, identical with the smallest of the three Wilmington specimens. Prior to this Agassiz (1840*b*), and Agassiz & Desor (1847), had actually referred to an adult specimen of *L. cenomanensis* but had attributed it to Lamarck's species *Holaster carinatus*. A plaster cast of this specimen, X69 in the Neuchâtel Museum, is in the British Museum (Natural History) and is very similar to the largest of the three Wilmington specimens. The adult form of *L. cenomanensis* was described and figured for the first time by Cotteau (1860) but under the name *H. suborbicularis*. The confusion over the identity of *H. suborbicularis* was not really cleared up until Lambert (1917) pointed out that Cotteau's specimen was simply an adult of the species previously described by d'Orbigny on the basis of a juvenile.

The sharp frontal carinae, gentle uniform curve of the anterior to dorsal surface in profile, the large and tall periproct and keel-shaped plastron make *L. cenomanensis* quite distinct from other holasterid species from Wilmington.

Labrotaxis tricarinata (Lambert 1924)

Pl. 32, figs 1–4; Pl. 33, fig. 3; Figs 63–64

1860 *Holaster suborbicularis* Cotteau & Triger: 198; pl. 33, figs 1–6 (*non* Defrance).
1873 *Holaster suborbicularis* de Loriol: 328 (*non* Defrance).
1881 *Holaster suborbicularis* Wright: 314; pl. 74, fig. 1 (*non* Defrance).
1917 *Holaster cenomanensis* d'Orbigny; Lambert: 207 (*partim*).
1924 *Holaster cenomanensis* d'Orbigny; Lambert & Thiéry: 403 (*partim*).
1924 *Holaster tricarinatus* Lambert, *in* Lambert & Thiéry: 404; pl. 10, figs 9, 10.

AMENDED DIAGNOSIS. A species of *Labrotaxis* with a well-developed frontal groove that is more or less vertical on the anterior face, curving sharply near the top where the adapical part of the anterior ambulacrum is more or less flush and faces dorsally. Peristome large, oval, rather sunken and lying moderately far back from the anterior border. In profile the test appears quadrate with a vertically truncated posterior and broad flat dorsal and ventral surfaces. The periproct is unusually large and the apical disc lies slightly anterior of the mid-point. Petals lanceolate, unsunken, with broad elongate pores: anterior petals with unequally developed columns of pores in adults.

MATERIAL. Sixteen specimens from the Wilmington pit (E.75585–7, E.80184–93, E.80602–3) were available. None, however, are well preserved and a detailed biometric study of this species was not attempted. A number of other specimens in the collection of Mr C. W. Wright have also been examined.

STRATIGRAPHICAL OCCURRENCE AND DISTRIBUTION. Seven specimens were collected *in situ*, all from the upper part of the Wilmington Sands from 358 cm to 653 cm below standard datum level. These therefore belong to the Lower Cenomanian. Elsewhere the species has also been found in the Middle Cenomanian Chloritic Marl at Chard, Somerset. Wright (1881) states that his '*Holaster suborbicularis*' is relatively common throughout southern England in Lower and Middle Cenomanian beds.

Description. *SHAPE AND SIZE.* The specimens available for study range 36–60 mm in length (mean = 47 mm; SD = 8·3; N = 9), though fragmentary smaller specimens are known. The test height is 56–67% of test length (mean = 60%; SD = 4·0; N = 9), and the test width 88–105% of test length (mean = 96%; SD = 3·1; N = 9). In outline the test is cordate. The widest part of the test is approximately mid-length, level with genital plates 1 and 4. The test in profile is characteristically subquadrate. The oral surface is more or less flat. The anterior face is almost vertical and curves fairly sharply to meet the dorsal surface, which in profile is almost flat. The posterior is sharply truncated and may even be very slightly undercut. The highest point of the test coincides with the apical disc and lies very slightly anterior of the mid-line. Viewed from the anterior, the dorsal surface slopes gently away from the mid-line and the frontal ambulacrum forms a narrow flat zone apically.

The frontal groove is well developed and there is a moderately sharp carina on adjacent interambulacral zones. At the ambitus the depth of the frontal groove is 5–8% of the test length (mean = 7%). It is well developed on the anterior surface and continues orally up to the peristome. Adapically, however, it disappears as ambulacrum III curves sharply to face almost vertically upwards, and here lies more or less flush with adjacent interambulacra. The plastron is gently but unmistakably keeled along the mid-line.

APICAL DISC. The apical disc is three times as long as it is broad and lies slightly anterior of the mid-line. Its length is 12–15% of the test length, and the anterior edge lies at 30–38% of the test length from the anterior border of the test (mean = 35%; SD = 1·1; N = 9). The exact arrangement of plates in the apical disc is variable (Fig. 63). Ocular plates II and IV abut along the median suture and are separated from ocular plates I and V by genital plates 1 and 4. The madreporic plate (genital 2) is not noticeably larger than the other genital plates and is largely covered by small pores. Gonopores are large and circular and lie towards the outer edge of genital plates.

AMBULACRA. The anterior ambulacrum is non-petaloid and anteriorly lies in a frontal groove which is moderately broad and parallel-sided. The pores in ambulacrum III are small oblique isopores with a prominent ridge-like interporal partition. The periporal attachment area is circular. These isopores are uniform in size from the ambitus to the apex. They are most densely spaced apically in the flat, upward-facing region of ambulacrum III and become progressively more widely spaced in the vertical part of the ambulacrum III adorally.

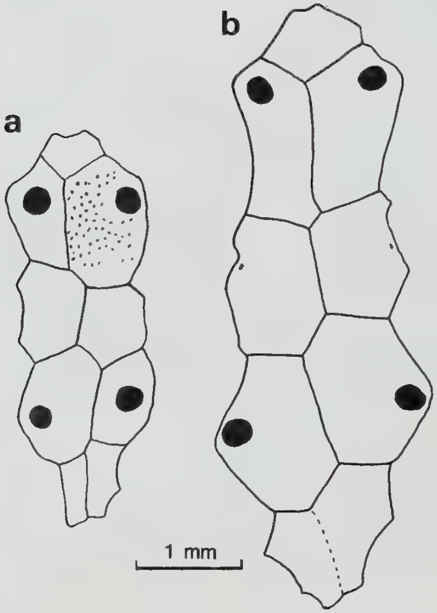


Fig. 63 Camera lucida drawings of apical disc plating in *Labrotaxis tricarinata* from the Lower Cenomanian of Wilmington: a, E.80187; b, E.80193.

The ambulacral plates around the mouth have large isopores like those in the phyllodes of other holasterids. There are three per column in ambulacrum III, four in ambulacra II and IV and three or four in ambulacra I and V. The number of pores in a complete column cannot be determined.

Both anterior and posterior paired petals are flush with the surface of the test. The anterior pair diverge at an angle of 130° and extend *c.* 80% of the distance to the ambitus. The petals are open at the base and taper slightly adapically. In each column the petal pores become gradually smaller and more widely spaced towards the ambitus, and thus there is no clearly defined limit to the petal. Plate addition appears to cease by the time the test reaches approximately 45 mm in length, since from 45 mm to 60 mm test length the anterior petal contains 35–37 pores per column and the posterior petal about 30. In the anterior paired petals the posterior column is slightly longer and contains noticeably broader petal pores than the anterior column. The pores are elongate, conjugate anisopores with slit-like pores, and adjacent anisopores are separated by a single row of miliary tubercles. The pores of the anterior column are similar but only about half the width. In an individual 50 mm in length the posterior anisopores are 2·0 mm in breadth, the anterior anisopores 1·05 mm in breadth and the interporiferous zone 2·0 mm. However, a small number of specimens, generally rather small, have much less well developed petal pores. In these the pores are circumflexed and conjugate isopores and the anterior column is only very slightly narrower than the posterior column (Pl. 32, fig. 1). The anterior column of petal pores in all specimens is generally only about 90% of the length of the posterior column.

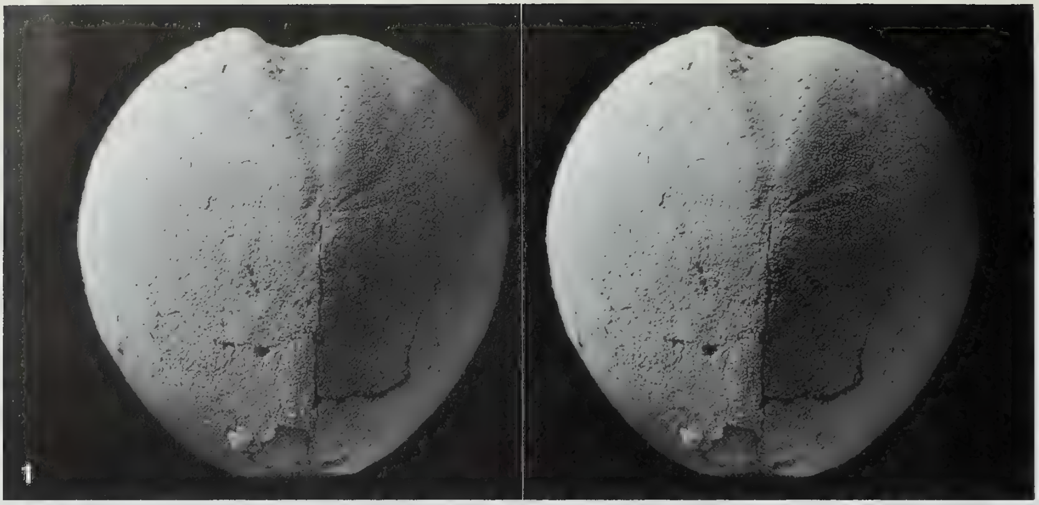
The posterior petals are shorter than the anterior petals and extend only 60–70% of the distance to the ambitus. The petal pores are like those of the anterior petals, although the difference in pore-zone width between anterior and posterior columns in the posterior petals is much less marked. The angle inscribed posteriorly by the two posterior petals is 70°. In both anterior and posterior petals, the anterior column of pores forms a straight line whereas the posterior column is very slightly flexed.

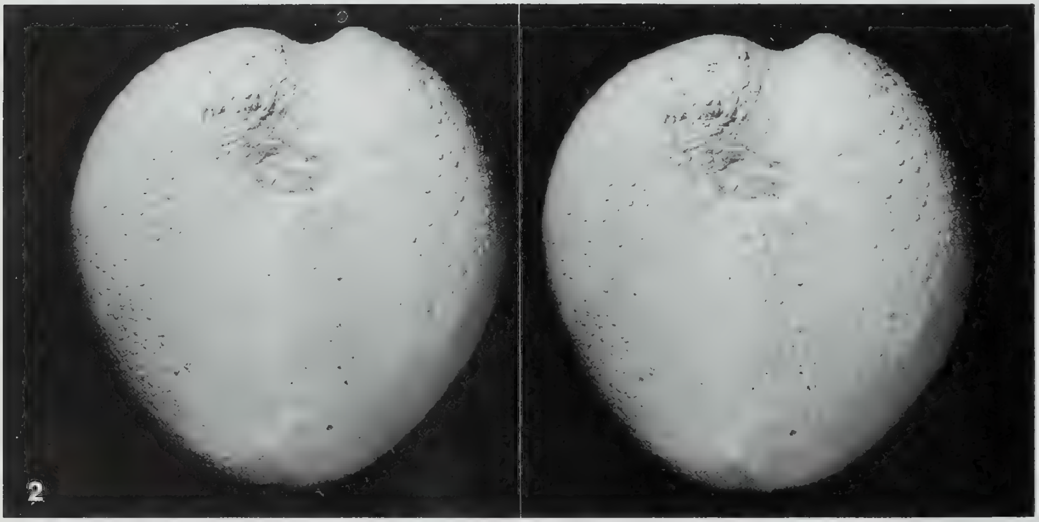
INTERAMBULACRA. Total numbers of plates per column cannot be gauged. The plastron is meridosternous and there is a slightly zigzagged median ridge. The plates of the posterior interambulacrum are large and triangular. These almost, but not quite, extend across the full width of the plastron (Fig. 64). Except for the labral plate, plastron plates are arranged alternately. The labral plate is small and triangular with a curved posterior edge (Fig. 64). The width of the plastron is 28–31% of the test width (mean = 30%; SD = 1·2; N = 5). Plastron tubercles extend to the very lip of the peristome. These tubercles are largest marginally and become smaller towards the mid-line. In other interambulacra a single triangular plate reaches the peristome.

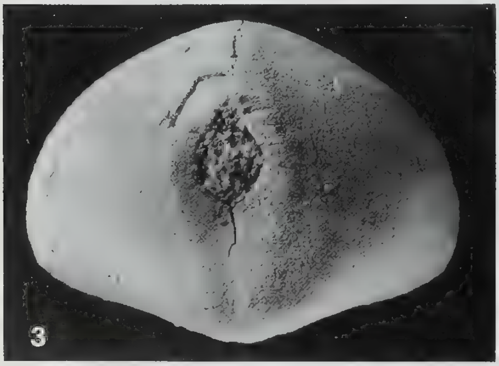
PERISTOME. The peristome lies near the anterior border and faces obliquely towards the anterior. Its length is 7–9% of the test length (mean = 8%; SD = 0·5; N = 4) and its width is 1·8–2·4 of the length (mean = 2·2; SD = 0·3; N = 4). The peristome is oval in outline with a broad, straight anterior and posterior edge. The anterior edge of the peristome lies 21–24% of the test length from the anterior of the test (mean = 22·5%; SD = 1·3; N = 4).

PERIPROCT. The periproct is seen in very few specimens. It is large and oval and lies at about mid-height or slightly above. In outline it is weakly pointed both at the top and bottom and is slightly taller than broad. The height of the periproct is 30–35% of the test height and the base of the periproct lies at 30–36% of the test height above the base of the test (mean = 34%; SD = 4·0; N = 4). Beneath the periproct, there is a distinct flattened zone (Pl. 32, fig. 3).

TUBERCULATION. Tubercles over most of the dorsal surface are small and inconspicuous. There is a dense covering of small tubercles, around 0·3 mm in diameter and with symmetrical areoles, with numerous miliaries scattered in between. Larger tubercles, up to twice the size of other dorsal tubercles, are found on the inward-facing interambulacral zones of the frontal groove. In larger specimens there are two or three such large tubercles abreast on each side, though they are never regularly arranged. These tubercles are symmetrically crenulate and have a more or less symmetrical areole. They face obliquely across the frontal groove. In


1


2


3

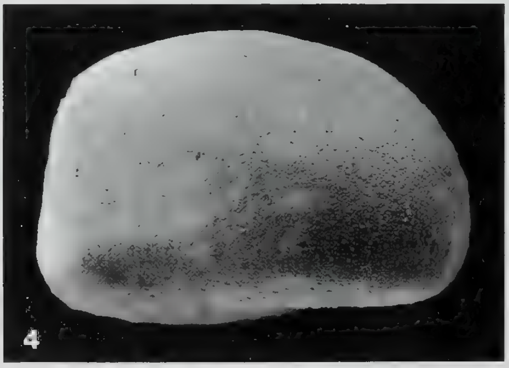

4

Plate 34

Labrotaxis cenomanensis (d'Orbigny)

Figs 1–4 E.80621: 1, apical; 2, oral; 3, posterior; 4, lateral, anterior to right. Basal part of the Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 3).

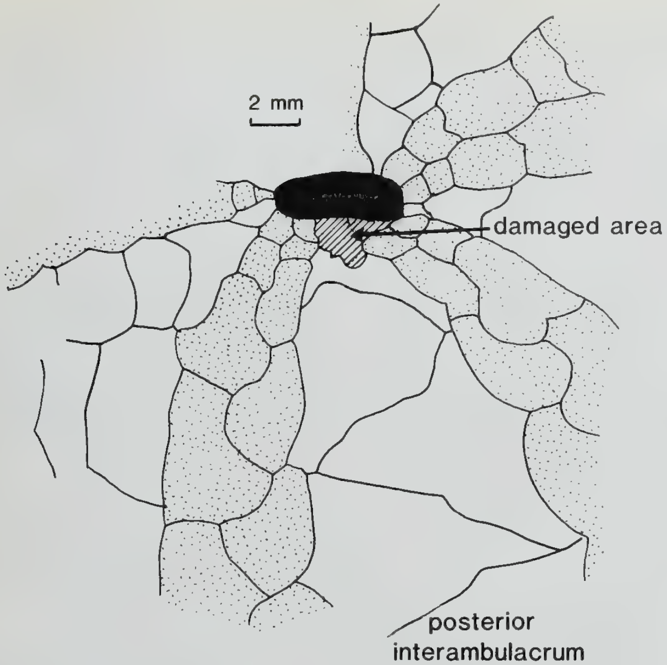


Fig. 64 Camera lucida drawing of the oral plating in *Labrotaxis tricarinata* (E.80189) from the Lower Cenomanian of Wilmington. Peristome shown in solid black.

interambulacra 2 and 3, larger tubercles are usually also present immediately adjacent to the apical system.

Within the ambulacral groove, ambulacral plates from the ambitus adapically are densely covered with miliary tubercles. A larger tubercle occurs on each plate immediately perradial to the isopore and a second, slightly smaller tubercle may occur nearer to the mid-line (Pl. 33, fig. 3).

There is no trace of marginal fasciole. On the oral surface the tubercles on the plastron are relatively large and are closely packed together. Smaller tubercles are present on the node at the growth centre of each plate and tubercles continue right up to the peristomial lip. The areoles of these tubercles are somewhat enlarged to the posterior side of the boss. Lateroventral tubercles are moderately dense and have an areole enlargement towards the lateroposterior. The periplastron region has only a light scattering of miliary tubercles. The anterior face of the test, flanking either side of the frontal groove, has tubercles slightly stouter than those present elsewhere above the ambitus.

REMARKS. This species was for a long time confused with *H. suborbicularis* (Brongniart) and *L. cenomanensis* (d'Orbigny). The species name was first proposed by Lambert (*in* Lambert & Thiéry 1924). Lambert based his species on what appears to be a juvenile with a slightly depressed apical system, but the characteristic quadratic profile of the test is quite evident from his figure. An almost identical specimen to the one figured by Lambert is in C. W. Wright's collection of Wilmington echinoids (C. W. Wright no. 2440). Unfortunately almost all the specimens from Wilmington are crushed and distorted to a greater or lesser extent and it is impossible to get an accurate quantitative estimate of the variation within the species. There does, however, appear to be a considerable range of shape, with individuals having a test height of anywhere between 50% and 79% of the test length.

L. tricarinata is different in profile from *H. suborbicularis*, although the two have often been confused. *L. tricarinata* has a large periproct just visible from above and a long flat or gently convex dorsal surface. The test, in profile, curves sharply between the flattened dorsal surface and the gently convex and steep anterior face, giving the test a quadrangular profile. *H. suborbicularis*, in contrast, has a strongly vaulted dorsal surface and in profile the test curves uniformly from the apex round to the anterior ambitus. Petal pores appear to be better developed in adult *L. tricarinata* and the anterior paired ambulacra have more unequal columns of petal pores than in a similar-sized *H. suborbicularis*.

Labrotaxis cenomanensis (d'Orbigny), which is described on p. 158, differs in being much more tumid dorsally, in having a valuted dorsal surface and in having a less well developed frontal groove.

L. tricarinata shows an unusually marked variation in petal pore development. The majority of individuals have in the anterior paired petals a posterior column with straight, elongate isopores that are twice as broad as those in the anterior column. However, in all the smaller individuals and in one or two of the moderate-sized ones the pores are smaller and circumflexed and the two columns of pores are less unequal. In other respects the two forms are indistinguishable and the differences may simply be due to differences in age and size.

The species was first reported in Britain by Wright (1881) under the name *H. suborbicularis*. He recorded it as being moderately common.

Genus ***CARDIASTER*** Forbes, 1850*a*

Cardiaster truncatus (Goldfuss 1829)

Pl. 19, figs 5–7

1829	*Spatangus truncatus* Goldfuss: 152; pl. 47, fig. 11.
1850*a*	*Cardiaster pygmaeus* Forbes: 444 [*nomen nudum*].
1852	*Cardiaster pygmaeus* Forbes; Forbes: 4; pl. 9.
1876	*Cardiaster pygmaeus* Forbes; Cotteau: 411; pl. 74, figs 5–8 (gives full synonomy of earlier authors).
1881	*Cardiaster pygmaeus* Forbes; Wright: 301; pl. 69, fig. 1.
1882	*Holaster Icaunensis* Lambert: 153 (*non* Cotteau).
1888	*Cardiaster pygmaeus* Forbes; Lambert: 412.
1917	*Cardiaster truncatus* (Goldfuss) Lambert: 212.
1924	*Cardiaster truncatus* (Goldfuss); Lambert & Thiéry: 406.

MATERIAL. Two rather poorly preserved individuals (E.80195, E.80197) were collected *in situ* at Wilmington and the description given here is based on the first of these.

STRATIGRAPHICAL OCCURRENCE AND DISTRIBUTION. At Wilmington, the specimens came from 42 cm and 55 cm above the datum level at the base of the Middle Chalk and therefore are Lower Turonian in age. Elsewhere in Britain the species is found in beds of a similar age on the south Devon coast between Beer and Branscombe, and in Kent. Wright (1881) reported it from the Upper White Chalk of Dover, Kent, but this seems to be a mistake as the Dover specimens come from the Middle Chalk Melbourn Rock.

DESCRIPTION. *SHAPE AND SIZE*. This is a small cordate holasteroid, 18 mm in length and 16·2 mm in breadth (width = 90% of length). The widest part of the test is 7·4 mm from the anterior (41% of the test length) and behind this the test tapers posteriorly. The test is abruptly truncated at the posterior where the width is 6·5 mm (40% of the maximum test width). The anterior groove is broad and shallow and is 3·9 mm in breadth at the ambitus (24% of maximum test width) and 1·0 mm deep (5% of the test length). The anterior groove is deepest at the ambitus and gradually becomes shallower adapically. It also continues adorally up to the peristome. Carinae are present on either side of the frontal groove but are not well developed. The test height is 12·7 mm (71% of test length). The highest point of the test lies 8·9 mm from the anterior (49% of test length) and coincides with the apical disc. In profile the plastron is visible and the base is very slightly convex. The dorsal surface is almost flat, the posterior is abruptly and vertically truncated while the anterior is gently convex. In front view the flanks of the dorsal surface are moderately curved. The ambitus is 2·9 mm above the base of the test (23% of test height).

APICAL SYSTEM. In the Wilmington specimens the apical disc is damaged. It lies anterior of the middle of the test and the anterior border of the disc lies 5·5 mm from the anterior border of the test (39% of the test length). Specimens of this species from the south Devon coastal sections show typical holasterid apical disc plating.

AMBULACRA. The ambulacra are narrow and, except for ambulacrum III, are flush with the test surface. The pores in ambulacrum III are minuscule isopores set slightly oblique to the horizontal and with a narrow interporal partition. They are no larger than 0·1 mm in diameter. The remaining four ambulacra have an identical pore arrangement and are non-petaloid. Dorsal pores are small and unobtrusive. They are weakly circumflexed isopores 0·2 mm or so in width and with a narrow interporal partition. Anterior and posterior columns of pores are identical. There are 26 plates in ambulacrum II at 18 mm test length.

INTERAMBULACRA. These are broad at the ambitus. There is a weak carina on either side of the frontal groove. The posterior interambulacrum is weakly keeled along the mid-line on the oral surface. Behind the small labral plate, plastron plating is arranged biserially, although each plate extends almost to the other side of the plastron. Anteriorly, interambulacra 2 and 3 are noticeably convex whereas the rest of the base is rather more planar. There is a very slight heel to the test in the subanal region.

PERIPROCT. The periproct is surprisingly large and is 4·0 mm in height (31% of the test height) and 2·6 mm in width (65% of its height). It is slightly angular in outline and comes to a weak point adorally. The periproct lies at about mid-height and its base lies 4·1 mm above the base of the test (at 32% of the test height).

PERISTOME. This is also fairly large, being 1·2 mm in length (7% of the length of the test) and 2·6 mm in breadth (2·1 times the length). It is broadly oval in outline with a weakly convex posterior border and a more strongly curved anterior border. There is no labral projection over the peristome. The anterior edge of the peristome lies 4·2 mm from the anterior border (23% of the test length).

TUBERCULATION. Dorsal tubercles are minute and uniform in size. Miliary tubercles are abundantly scattered amongst the primary tubercles. Tubercles are noticeably larger, though still small, adjacent to the anterior ambulacrum along the outer edges of the frontal groove.

REMARKS. This species was first figured and described by Goldfuss (1829) and was first reported in Britain under the name *Cardiaster pygmaeus* by Forbes (1850*a*; 1852). It is a well-known species in the Turonian of north-western Europe. It never grew much larger than 20–25 mm in length and these represent sexually mature individuals since they have open gonopores at this size. They have a very distinct shape and are easily distinguished from other species.

Genus ***CARDIOTAXIS*** Lambert, 1917

Cardiotaxis cf. ***cretacea*** (Sorignet 1850)

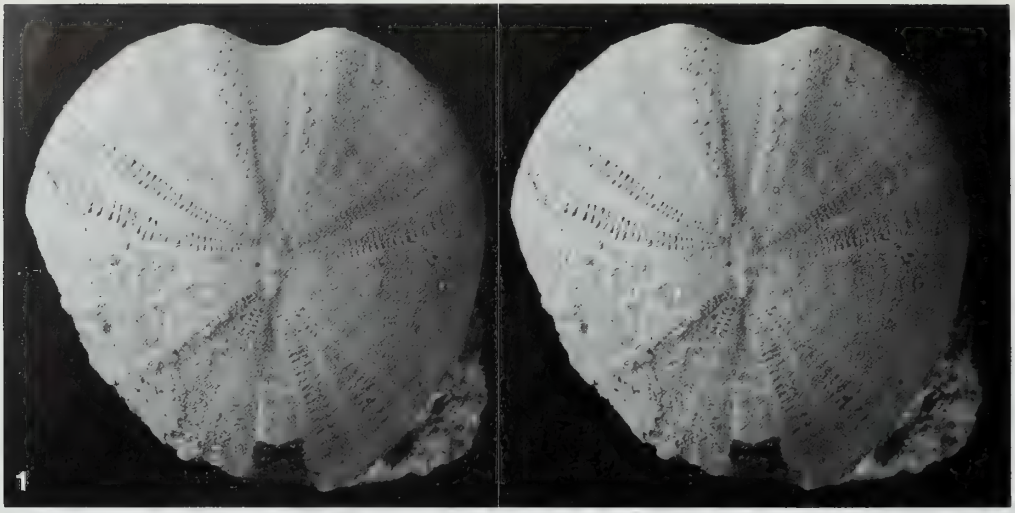
Pl. 35, figs 2–4; Fig. 65

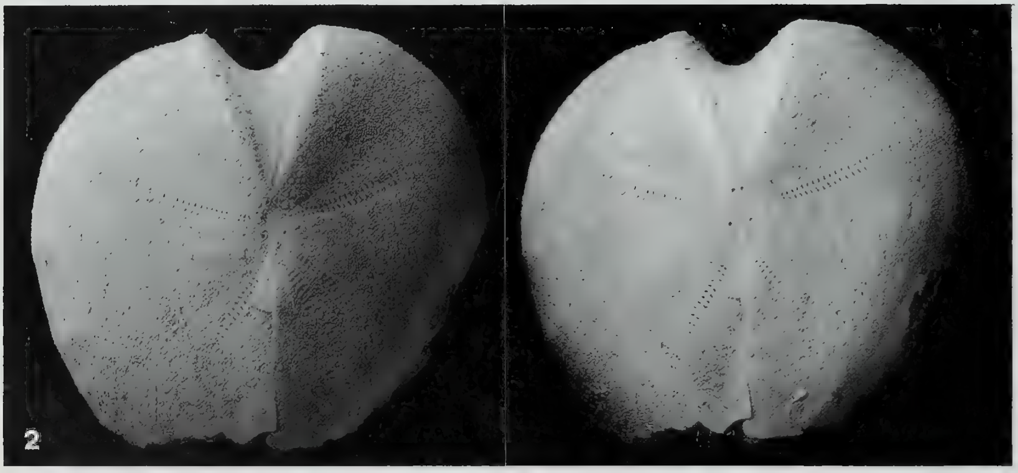
cf. 1850 *Holaster cretaceus* Sorignet: 69.
cf. 1888 *Cardiaster cretaceus* (Sorignet) Lambert: 416; pl. 8, figs 19–21.
cf. 1917 *Cardiaster* (*Cardiotaxis*) *cretaceus* (Sorignet); Lambert: 215.
cf. 1924 *Cardiotaxis cretaceus* (Sorignet) Lambert & Thiéry: 406.

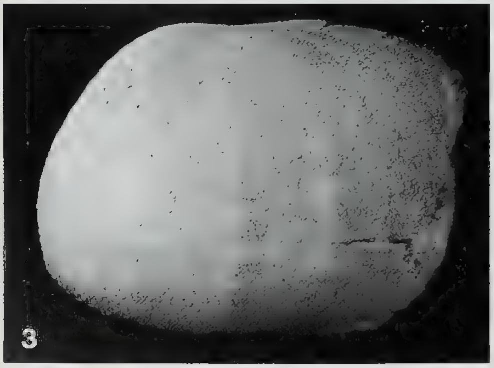
MATERIAL. Only one somewhat damaged specimen was collected at Wilmington (E.80196) and is described here.

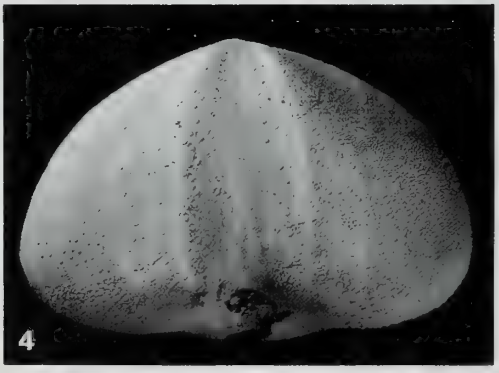
STRATIGRAPHICAL OCCURRENCE AND DISTRIBUTION. The Wilmington specimen was collected 97 cm above the datum level at the base of the Middle Chalk and therefore comes from the Lower Turonian. The species is not uncommon in beds of a similar age throughout south Devon.

DESCRIPTION. *SHAPE AND SIZE.* The test is cordiform in outline with the right anterior side protruding slightly further than the left. Test length is unknown as the posterior of the specimen is missing, but the test gives an appearance of being broadly circular and length unlikely to


1


2


3


4

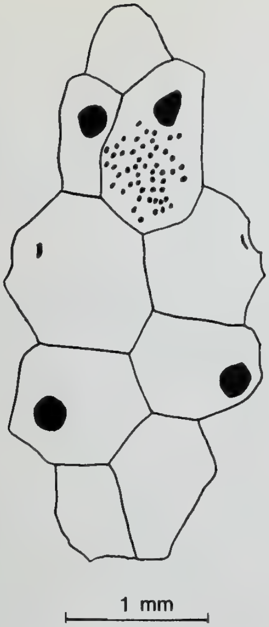


Fig. 65 Camera lucida drawing of apical disc plating of *Cardiaster* cf. *cretacea* (E.80196) from the Lower Turonian of Wilmington.

be very much greater than test width. The test width is 29 mm and its height 19 mm. A well developed carina lies on either side of the frontal groove and extends to the apical disc. The tallest point on the test is formed by the carina and lies slightly anterior of the apical disc and the apical disc in profile is slightly depressed. The frontal groove is broad and deep and, at the ambitus, is 2·5 mm deep and 7·3 mm broad. It is deepest ambitally and becomes shallower adapically, though it never quite disappears. The groove continues adorally to the peristome. In profile the test has a flat base and top. The anterior face rises more or less perpendicular to the base but curves gradually adapically.

APICAL DISC. The apical disc is elongate, being 4·3 mm long and 1·6 mm at its widest (width is 38% of the length). Ocular plates II and IV are in contact along the mid-line and are larger than any of the other plates (Fig. 65). Genital plate 3 is very noticeably smaller than the other genital plates. The anterior two gonopores lie close together whereas the posterior two gonopores are much more widely separated. The front of the apical disc lies 12·8 mm back from the anterior edge of the test, and the disc lies obviously anterior of the mid-line.

AMBULACRA. The frontal ambulacrum is sunken and non-petaloid. Ambulacral pores are small, oblique isopores with a well-defined neural canal, tall interporal partition and a circular periporal area. The isopores are closely spaced adapically, and become more widely spaced adambitally where the pores are also slightly smaller. Adorally there are larger isopores for the phyllode tube feet. There are three phyllode pores per column in ambulacrum III, four in ambulacra II and IV and three in ambulacra I and V. There is a total of 28 plates in ambulacrum III.

Plate 35

Holaster revestensis Lambert

Fig. 1 E.80624, apical. Basal part of the Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 2).

Cardiotaxis cf. *cretacea* (Sorignet)

Figs 2–4 E.80196: 2, apical; 3, lateral, anterior to right; 4, posterior. Lower Turonian, White Hart sand pit, Wilmington, Devon (× 2).

The anterior paired petals are open distally and taper adapically. There is no sharply defined base to the petals. The angle defined by these petals is 125°. The columns of pores are unequal both in length and in pore development. There are 27 broad, straight conjugate anisopores, 0·7 mm in breadth at their widest, in the posterior column. The anterior column has much less well developed conjugate isopores lacking a periporal rim. These are very small adapically and adambitally and at their broadest are only 0·3 mm broad. The interporal zone is moderately broad and at mid-length measures 1·3 mm. Successive pores in both columns are separated by single rows of miliary tubercles (Pl. 35, fig. 2). The anterior column of petal pores is slightly shorter than the posterior column. The petals extend approximately $\frac{2}{3}$ of the distance to the ambitus.

The posterior petals are a little shorter (approximately 75% of the anterior petals) and consist of 19 pores per column. They are similar to the anterior petals in column length and pore development. The posterior column of petal pores is slightly longer and consists of broad, straight anisopores up to 0·6 mm in width. The anterior column has only poorly developed isopores up to 0·25 mm in width. The angle formed between the posterior petals is 90°. All pores between the petals and the phyllode pores are isopores, but they are minute and very difficult to locate.

INTERAMBULACRA. The carinae bordering the frontal groove are well marked and raised slightly above the general level of the test adapically. There is also a weak dorsal carina in the posterior interambulacrum. Plastron plating is not seen.

PERISTOME. The peristome is oval in outline and faces obliquely forwards towards the frontal groove. In length it is about 1·6 mm and in breadth 3·7 mm (2·3 times the length). The anterior edge is gently curved and lies at the base of the anterior groove 7·0 mm from the anterior of the test.

PERIPROCT. Not seen.

TUBERCULATION. Dorsal tubercles are small (about 0·3 mm in diameter), relatively densely packed and with many miliaries scattered amongst them. Larger tubercles are present along the dorsal posterior carina adapically. They are also present along the two anterior carinae. The largest tubercles, up to 0·6 mm in diameter, line the inner edge of the frontal groove and face obliquely across it. Tuberculation on the anterior-facing zones either side of the frontal groove is also slightly coarser than tuberculation elsewhere. At the ambitus there is a sharp break between the dorsal tubercles and the lateroventral tubercles coinciding with the marginal fasciole. This fasciole is up to 1·7 mm in width and is composed of discrete rows of miliary tubercles which are not as densely packed as those in the fascioles of most spatangoids. Scattered within the fasciole are occasional tubercles. The marginal fasciole is best developed posterior of the mid-line and it dwindles and disappears anteriorly.

REMARKS. Unfortunately this specimen is damaged and details of plastron plating and the periproct have been lost. It is therefore impossible to be certain about the identification, but as far as can be seen it is identical to *Cardiotaxis cretacea* (Sorignet), as described by Lambert (1917), a species which is relatively common in beds of the same age on the south Devon coast.

Order **SPATANGOIDA** Claus, 1876

Family **MICRASTERIDAE** Lambert, 1920

Genus ***MICRASTER*** Agassiz, 1836

Micraster distinctus Agassiz & Desor 1847

Pl. 38, fig. 3; Pl. 39, figs 1–4; Figs 66–67

1840*b* *Micraster distinctus* Agassiz: 2 [*nomen dubium*].
1847 *Micraster distinctus* Agassiz; Agassiz & Desor: 23.
1854 *Epiaster distinctus* ('Agassiz') d'Orbigny: 196; pl. 861.
1894 *Epiaster distinctus* ('Agassiz'); Lambert: 66 [see also for full synonymy].
1961 *Epiaster distinctus* d'Orbigny; Cayeux: 10; fig. 4.

MATERIAL. Three specimens of this species are known from Wilmington, only one of which was collected *in situ*. The description is based on the two better-preserved specimens, E.80265 and IGS GSM.108782. The third specimen (E.80626) is too crushed and damaged to be of use.

STRATIGRAPHICAL OCCURRENCE AND DISTRIBUTION. At Wilmington the single specimen found *in situ* came from near the base of the Grizzle, 301 cm below standard datum. The preservation and nature of the adhering sediment show without doubt that the other two specimens also came from either the Wilmington Sands or the Grizzle. All are therefore Lower Cenomanian in age.

DESCRIPTION. *SHAPE AND SIZE*. The test is cordate in outline with an almost flat interior and a roundly truncated posterior. The ambulacra are sunken adapically but at the ambitus the frontal ambulacral groove is almost absent and the test is only very feebly concave here. The two reasonably well preserved specimens are 37·0 mm and 44·5 mm in length and 38·6 mm and 41·5 mm in width respectively (test width is 93% and 103% of the test length). In height the tests are 24·6 mm and 30·0 mm (66% and 67% of the test length). The widest point on the test lies 45–46% of the test length from the anterior border and the tallest point on the test lies posterior to the apical disc at 65–68% of the test length from the anterior border. Both specimens have a very slightly asymmetrical outline with the right anterior side of the test bulging a little further than the left anterior side. The truncated posterior zone of the test is about 45% of the maximum test width.

In profile the test is broadly wedge-shaped. The dorsal surface slopes anteriorly and the smooth curve of the test continues around the anterior. The posterior of the test is steeply truncated and the subanal region protrudes backwards in a heel which comes to a rounded point near the base. In anterior view the apical part of the test is flat while the flanks curve smoothly down to the ambitus, which lies at about mid-height. The peristome is clearly visible from the front.

APICAL DISC. The apical disc is tetrabasal and ethmophract. It is compact and roughly circular in outline. It lies centrally, its anterior edge 45–48% of the test length from the anterior border of the test. It is slightly sunken below the adjacent interambulacral zones. The madreporite (genital plate 2) is only slightly larger than the other genital plates and is in contact with them all (Fig. 66). Genital plates 1 and 4 abut and ocular plates I and V are also adjacent. All four genital plates have a gonopore. The posterior bulge of genital plate 2 which almost separates genital plates 1 and 4 is characteristic of early species of *Micraster*, as illustrated by Stokes (1977: fig. 1).

AMBULACRA. All five ambulacra are sunken adapically, and the petals are more or less straight, taper adapically and remain open distally, though they are very slightly constricted. They extend about $\frac{2}{3}$ of the distance to the ambitus and their length is 33–34% of the test length. The petals at their widest are 26–30% of the petal length. The pores are conjugate isopores with an interporal partition forming over 50% of their width. The two pores are slit-like and the isopores are situated on the walls of the petals. The perradial interporal zone

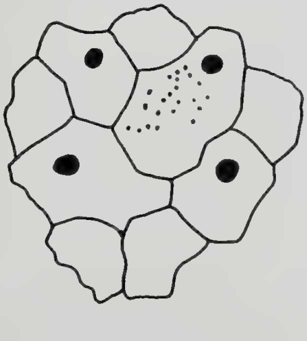


Fig. 66 Camera lucida drawing of the apical disc of *Micraster distinctus* (E.80625) from the Lower Cenomanian of Wilmington.

forms the flat floor of the sunken petals. This is smooth and forms 37–38% of the petal width at its widest. The petals form an angle of 115° to the anterior and in both specimens there are 33 isopores per column in the anterior petals.

The posterior paired petals are shorter than the anterior pair and slightly less sunken. They are 21–24% of the test length in length and in width are 36% of the petal length. The petals extend approximately 50% of the distance to the ambitus. The isopores of the posterior petals are similar to those of the anterior petals and there are 26 or 27 isopores per column. The posterior petals are straight and form an angle to the posterior of about 50°. The perradial interporal zone is smooth and at its widest forms 34–35% of the petal width. Below the petals the pores become widely spaced and minute but remain isopores.

The anterior ambulacrum is sunken adapically but by the ambitus it is almost flush. Adapically there are prominent isopores, about 0·7 mm in width. These have relatively large, oval pores with a narrow, slightly raised interporal partition. There are 13 to 15 such pores, moderately widely spaced in each column. Below this the pores become noticeably smaller and further apart. This adapical region extends for about 55–60% of the distance to the ambitus and has a width 33–34% of its length. The floor of the ambulacral groove is largely covered in miliary tubercles, but scattered primary tubercles are also present.

Ambulacral pores on the oral surface are small and insignificant isopores except adjacent to the peristome. Here there are large round isopores each with a circular attachment area and a prominent interporal bulge. There are 2 or 3 phyllode pores per column in ambulacrum III, 5 or 6 in ambulacra II and IV and 4 or 5 in ambulacra I and V.

The isopores in the subanal region are enlarged in comparison to adjacent isopores, but they are not well developed.

INTERAMBULACRA. The adapical regions of all five interambulacra are elevated to form wedge-shaped ridges between the petals. In particular the posterior interambulacrum forms a low crest behind the apical disc. On the oral surface all five interambulacra reach the peristome. The plastron is relatively large and the labral plate triangular with a concave posterior (Fig. 67). Unfortunately the position of the suture between plates 2a and 2b on the plastron cannot be determined.

PERIPROCT. This is oval and slightly pointed in outline, and just visible from above. At a test length of 44·6 mm, the periproct has a height of 6·7 mm (22% of the test height) and lies a little above mid-height. The width of the periproct is 61% of its height. The base of the periproct lies at 53% of the test height above the base of the test.

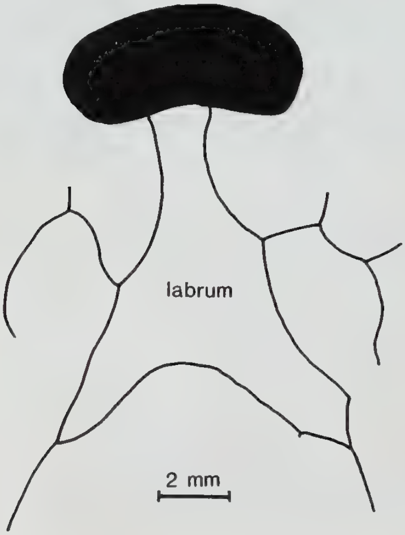


Fig. 67 Camera lucida drawing of the oral plating of *Micraster distinctus* (E.80625) from the Lower Cenomanian of Wilmington. Peristome shown in solid black.

PERISTOME. The peristome is broader than long with a convex anterior border and an equally concave posterior border. In length the peristome is 8% of the test length and its width is a little over twice its length. The anterior edge of the peristome lies 23% of the test length from the anterior border of the test. The ambulacra are hardly sunken adjacent to the peristome and the labrum barely projects over the peristome. It is surrounded by a weak but obvious rim.

TUBERCULATION. Aboral tubercles are small (0·4 mm in diameter) and scattered with circular areoles. Miliary tubercles are abundant and densely packed between the primary tubercles. These miliary tubercles tend to be in patches with a discrete alignment, but no fascioles are present either dorsally or in the subanal region. Tubercles on the plastron are relatively large and densely packed without interspersed miliary tubercles. Areole enlargement towards the posterior is prominent. Lateroventral tubercles are similar in size but more widely spaced and without such a noticeable areole enlargement. The ambulacra on the oral surface are more or less smooth, showing weak surface pitting.

REMARKS. The name *Micraster distinctus* was first proposed by Agassiz (1840*b*) but this is a *nomen nudum*. The name became validated when Agassiz & Desor (1847) published a brief description. D'Orbigny (1854) described and figured material of this species from the Cenomanian of Normandy, firmly establishing its identity, and subsequent workers have had no difficulty in determining it. This species is assigned here to the genus *Micraster*, which it resembles in all features save for the total absence of a subanal fasciole. Previously, *Micraster*-like spatangoids lacking fascioles have usually been placed in the genus *Epiaster* d'Orbigny, which Stokes (1977) characterized as being generally small, rarely exceeding 60 mm in length, with a thin test and a pronounced subanal heel. However, there is a problem with the name *Epiaster*, which was first proposed by d'Orbigny in 1854. He, however, designated no type species and within that particular section of *Paléontologie Française* described three species of *Epiaster*, *E. polygonus*, *E. trigonalis* and *E. tumidus*. D'Orbigny slightly later went on to describe further species of *Epiaster*, including *E. crassissimus* Defrance. Lambert (1895) selected *E. crassissimus* as type species for the genus *Epiaster* but later rejected this choice (*in* Lambert & Thiéry 1924), presumably because *E. crassissimus* was not amongst those species d'Orbigny had originally placed in *Epiaster* at the time of its first publication. Lambert & Thiéry (1924) therefore substituted *Epiaster trigonalis* d'Orbigny as the type species of *Epiaster*. Stokes (1977) was thus wrong to resurrect *E. crassissimus* as the type species. Unfortunately, *E. trigonalis* is undoubtedly a species of *Heteraster* d'Orbigny 1855, having alternately small and large ambulacral pores in the frontal ambulacrum. *Epiaster* is thus synonymous with *Heteraster*. Until a thorough revision of these primitive spatangoids is undertaken it seems best to retain this species within the genus *Micraster*.

Micraster distinctus most closely resembles *M. michelini* Agassiz, from the Turonian. Indeed, the two forms differ only in that *M. michelini* has slightly shorter and deeper petals and has a subanal fasciole. *M. distinctus* has not previously been reported from Britain.

Family **HEMIASTERIDAE** Clark, 1917

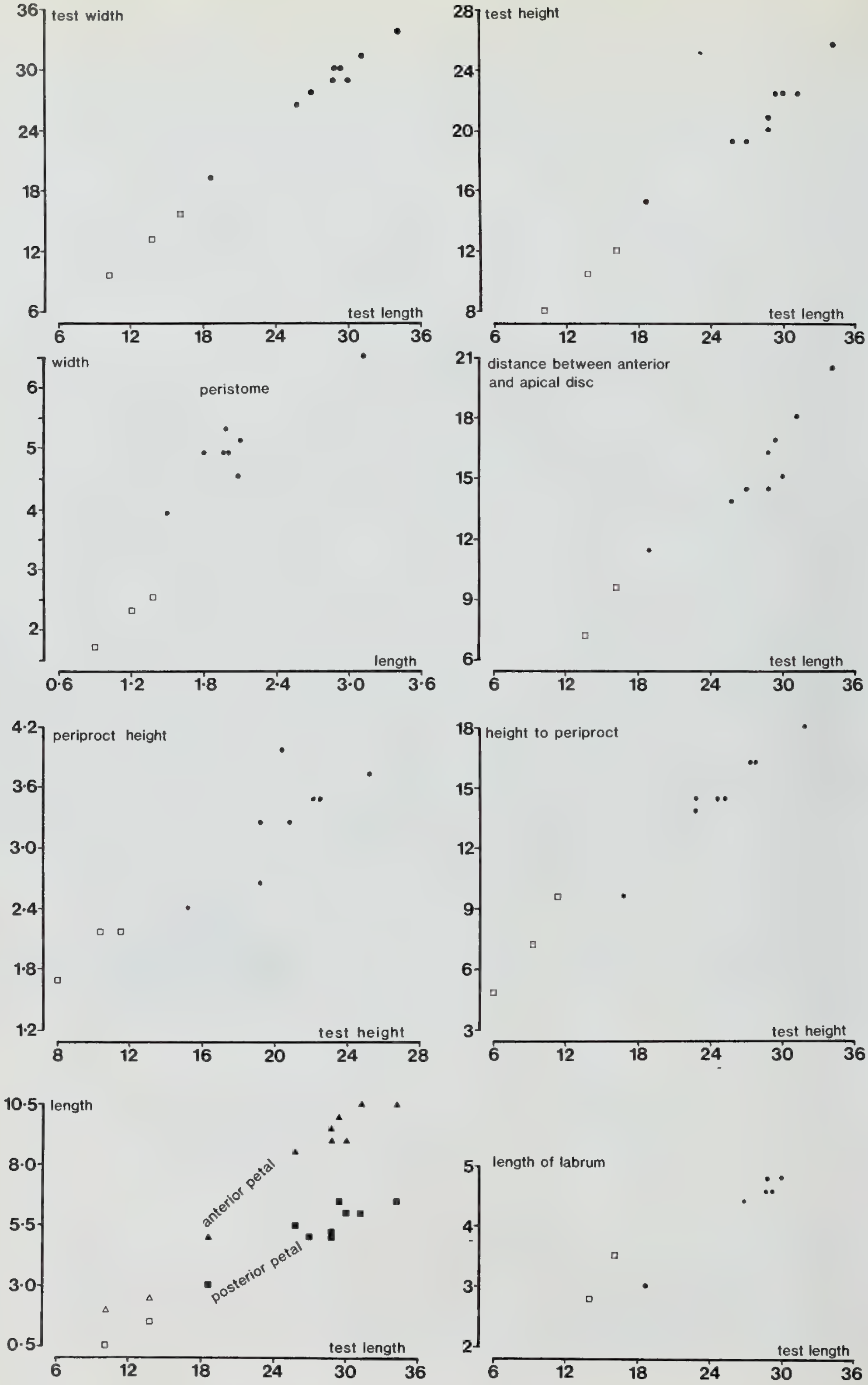
Genus ***HEMIASTER*** Agassiz, *in* Agassiz & Desor, 1847

Subgenus ***HEMIASTER*** Agassiz, *in* Agassiz & Desor, 1847

Hemiaster* (*Hemiaster*) *bufo (Brongniart 1822)

Pl. 36, figs 1–4; Figs 68, 69a, 70

1822 *Spatangus Bufo* Brongniart: 84, 289; pl. 5, fig. 4.
1847 *Hemiaster Bufo* (Brongniart) Desor, *in* Agassiz & Desor: 122.
1854 *Hemiaster Bufo* (Brongniart); d'Orbigny: 227; pl. 873, figs 1–10.
1859 *Hemiaster bufo* (Brongniart); Cotteau & Triger: 208; pl. 24, figs 8, 9 (see also for full synonymy).
1905 *Hemiaster bufo* (Brongniart); Savin: 15.
1924 *Hemiaster* (*Hemiaster*) *bufo* (Brongniart); Lambert & Thiéry: 499.
1950 *Hemiaster bufo* (Brongniart); Mortensen: 380; fig. 272.


test width
36
30
24
18
12
6
test length
6
12
18
24
30
36
test height
28
24
20
16
12
8
test length
6
12
18
24
30
36
width
peristome
6
5
4
3
2
length
0·6
1·2
1·8
2·4
3·0
3·6
distance between anterior
and apical disc
21
18
15
12
9
6
test length
6
12
18
24
30
36
periproct height
4·2
3·6
3·0
2·4
1·8
1·2
test height
8
12
16
20
24
28
height to periproct
18
15
12
9
6
3
test height
6
12
18
24
30
36
length
10·5
8·0
5·5
3·0
0·5
anterior petal
posterior petal
test length
6
12
18
24
30
36
length of labrum
5
4
3
2
test length
6
12
18
24
30
36

1955 *Hemiaster bufo* (Brongniart); Szörényi: 123; pl. 22, figs 1–7, 11.
1965 *Hemiaster bufo* (Brongiart); Cayeux & Villoutreys: 23; fig. 10.
1966 *Hemiaster (Hemiaster) bufo* (Brongniart); Fischer: U558; fig. 442.1.

MATERIAL. Fourteen specimens of *H. bufo* were collected at Wilmington (E.76327, E.76615 and E.80630–41), of which six have accurate stratigraphical data. Nine more or less whole and uncrushed specimens (E.76327, E.76615 and E.80635–41) were measured for the biometric analysis.

STRATIGRAPHICAL OCCURRENCE AND DISTRIBUTION. At Wilmington five of the six specimens were collected near the boundary between the Wilmington Sands and the Grizzle, while the sixth came from the lower part of the Wilmington Sands. *H. bufo* thus ranges from 813 to 294 cm below standard datum, i.e. within the Lower Cenomanian. This species has not been previously reported from Britain, although it is a common species in the Lower Cenomanian of France.

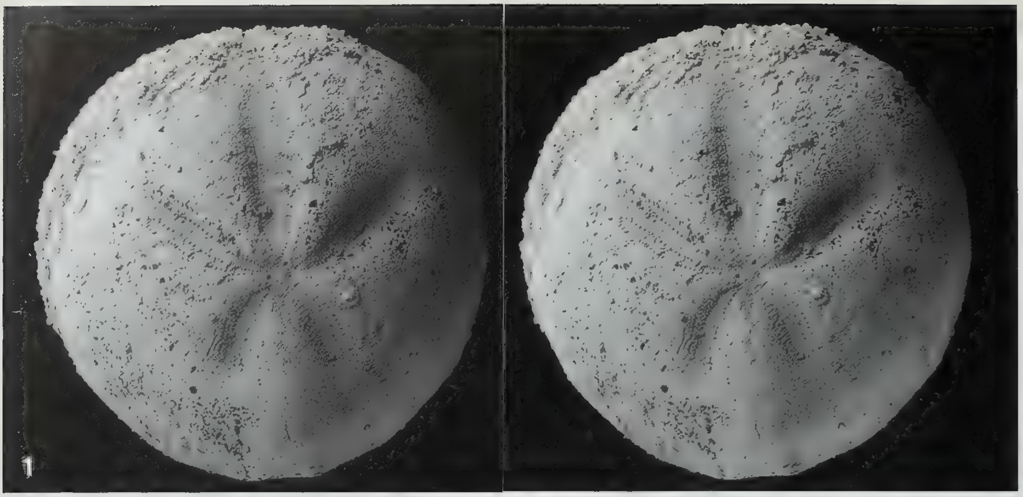
DESCRIPTION. *SIZE AND SHAPE*. The test ranges in size from 18·5 to 34·0 mm in length (mean = 28·1 mm; SD = 4·3; N = 9) and is subcordate in outline. It is very broad anteriorly and tapers to a rounded point posteriorly. The anterior edge is broad and straight without the slightest hint of a frontal sulcus at the ambitus. Test width is approximately the same as test length, ranging from 96–103% of the length (mean = 101%; SD = 1·0; N = 9) and the widest point on the test lies 49–51% of the test length from its anterior border (mean = 51%; SD = 1·3; N = 9). In profile the test is wedge-shaped, sloping uniformly from near the posterior to the anterior ambitus. The test height is 70–83% of the length of the test (mean = 74%; SD = 3·2; N = 9) and the tallest point lies 76–88% of the test length from the anterior border of the test (mean = 79%; SD = 0·3; N = 9). This coincides with a point midway between the apical disc and the periproct. The posterior is truncated almost vertically and the base is slightly convex. The ambitus lies 30–40% above the base of the test.

APICAL SYSTEM. The apical disc is small and compact and is roughly circular in outline (Fig. 69a). In an individual 28 mm in length the disc is 2·2 mm in diameter (8% of the test length). The four genital plates are in contact with one another centrally and are broadly similar in size, although genital plate 2 may be slightly larger. The gonopores are relatively large in adults and occupy much of each plate. They have not yet opened in an individual 18 mm in length. Ocular plates II, III and IV are small, triangular and separated from one another, whereas oculars I and V are more squarish and are in contact posteriorly. Hydropores are confined to genital plate 2. The apical disc lies 50–60% of the test length from the anterior border of the test (mean = 55%; SD = 3·9; N = 9).

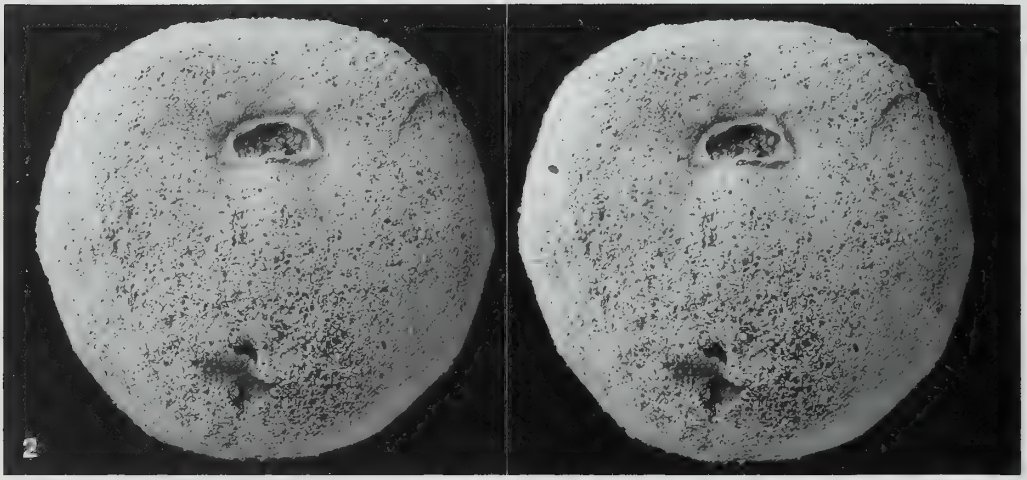
AMBULACRA. All five ambulacra are sunken adapically and the paired ambulacra are petaloid. The anterior ambulacrum is gently sunken adapically but becomes flush adambitally. It is moderately broad, 4 mm at the ambitus in a specimen 30 mm in length, and a little broader than the petals. The distance from the apex to where the fasciole crosses ambulacrum III is 50% of the test length at 30 mm. Ambulacral pores are moderately large adapically and become smaller and more widely spaced near the fasciole. The ambulacral pores are oblique isopores, 0·3 mm in diameter, with a circular attachment rim and a bulbous interporal partition. Adambitally, the ambulacral pores become minute unipores that are extremely difficult to find.

The anterior paired petals are 27–34% of the test length in length (mean = 31%; SD = 2·6; N = 9) and extend about 55% of the distance to the ambitus. They end slightly inside the fasciole, and are more or less straight although with a slight flexure adapically. The anterior angle between these petals is about 110–115°. There are 16 ambulacral pores per column at 18·5 mm test length, rising to 23 or 24 from 28 to 34 mm test length. The two columns of ambulacral pores are unequally developed with those in the posterior column being about $1\frac{1}{2}$ times as broad as those in the anterior column. All ambulacral pores are elongate and conju-

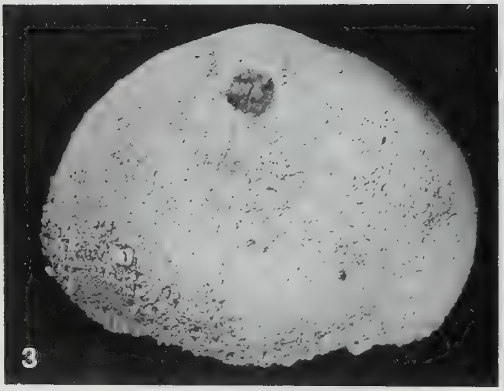
Fig. 68 Biometric data on *Hemiaster bufo* (●, ■, ▲) and *H. nasutulus* (□, △) from the Lower Cenomanian and Lower Turonian respectively of Wilmington.



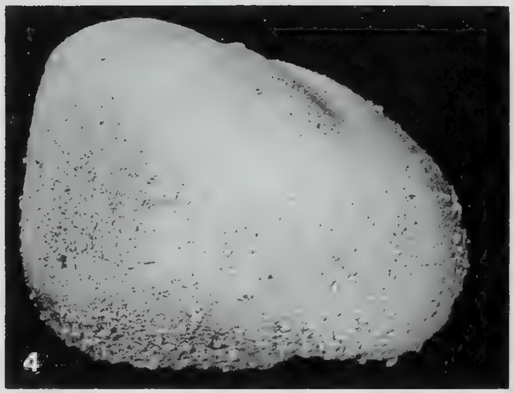
1



2



3



4

Plate 36

Hemiaster (*Hemiaster*) *bufo* (Brongniart)

Figs 1, 3, 4 E.81480: 1, apical; 3, posterior; 4, lateral, anterior to right. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 2).

Fig. 2 E.80636: oral. As last (× 2).

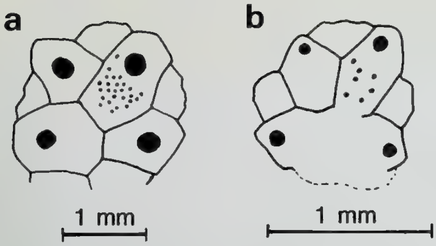


Fig. 69 Camera lucida drawings of apical disc plating in *Hemiaster* from Wilmington: a, *H. bufo*, E.80639; b, *H. nasutulus*, E.80628.

gate isopores with slit-like pores connected by a narrow, low ridge. The petals are open and unconstricted distally (Fig. 70a).

The posterior paired ambulacra are shorter than the anterior petals, measuring 57–67% of the anterior petals (mean = 62%; SD = 4·9; N = 9) and extend 50% of the distance to the ambitus. They are straight and form an angle of about 75° to the posterior. They measure 17–22% of the test length in length (mean = 19%; SD = 1·7; N = 9) and stop slightly before the peripetalous fasciole. The two columns of pores are approximately equal and are composed of elongate, conjugate isopores 0·7–0·8 mm in width at 30 mm test length. There are 10 pores per column in an individual 18·5mm in length, rising to 17 or 18 in individuals 29–34 mm in length. These petals are open distally.

Adorally, larger isopores with a circular attachment area and a bulbous interporal partition are found. There are 3 isopores per column in ambulacrum III, 4 or 5 per column in ambulacra II and IV and 3 or 4 per column in ambulacra I and V.

INTERAMBULACRA. The interambulacra are raised adapically and the posterior interambulacrum is particularly raised, forming a keel behind the apical disc. On the oral surface

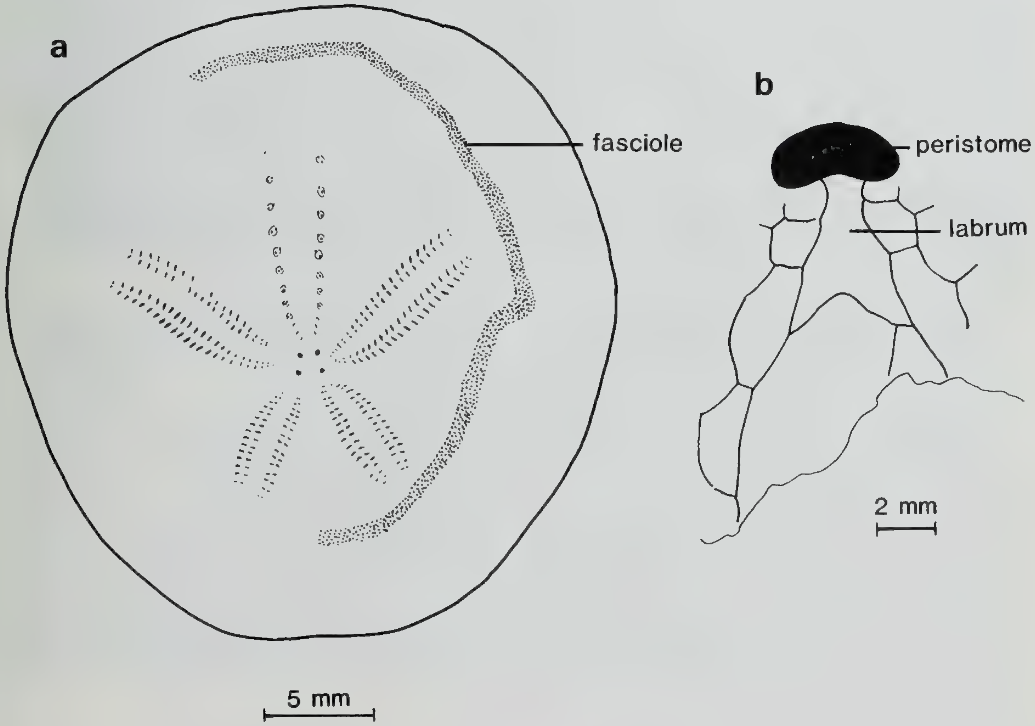


Fig. 70 Camera lucida drawings of *Hemiaster bufo* from the Lower Cenomanian of Wilmington: a, E.81480, adapical plating and fasciole outline; b, E.80638, oral plating.

the plastron is amphisternous with a long funnel-shaped labral plate with length 16–17% of the test length (mean = 16%; SD = 0·35; N = 6). The posterior border of this plate is strongly concave (Fig. 70b), while the anterior projects slightly over the peristome. Both sternal plates are in contact with the labral plate though plate 2b has only a narrow zone of contact. They are slightly more than twice the length of the labrum and become broader towards the posterior. The suture between plates 2a and 2b runs obliquely and meets the labral plate close to the right-hand side of the plastron.

PERIPROCT. The periproct is small and situated high on the posterior face. It is oval in outline, slightly taller than broad and 11–18% of the test height in height (mean = 15%; SD = 2·5; N = 9). The periproct width is 67–93% of its height (mean = 83%; SD = 7·6; N = 9). The base of the periproct lies 64–78% of the test height above the base of the test (mean = 71%; SD = 3·4; N = 9).

PERISTOME. The peristome is relatively large and is broader than long. In outline it is kidney-shaped, with a convex anterior edge and a concave posterior edge. The length of the peristome is 6–9% of the test length (mean = 7%; SD = 0·9; N = 8) and its width 2·1–2·7 times its length (mean = 2·2; SD = 0·2; N = 8). There is a very prominent rim and groove surrounding the peristome. The anterior edge of the peristome lies 21–29% of the test length from the anterior border of the test (mean = 25%; SD = 2·5; N = 9).

TUBERCULATION. A large peripetalous fasciole of close-packed miliary tubercles some ten to twelve abreast is present. It is roughly oval in outline but with a small kink just posterior to the anterior paired petals (Fig. 70a). In an individual 29 mm in length the length of the peripetalous fasciole is 80% of the test length and its width is 90% of its length. The petals stop slightly before they reach the fasciole. Aboral tuberculation is similar on either side of the fasciole. The adapical interambulacral ridges have slightly coarser tubercles and there are larger and more closely packed tubercles bordering ambulacrum III. Elsewhere tubercles are small and moderately densely packed with a pronounced areole enlargement on the anterior side of the tubercle. Scattered miliary tubercles occur amongst these. On the oral surface plastron tubercles are densely packed on the sternal plates but do not extend onto the labrum. The periplastronal zones are broad and tubercle-free although the surface of the plates are rather granular here. Lateroventral tubercles are moderately large but relatively sparse. In the subanal region there are a pair of very densely tuberculated zones facing posteriorly; in life *H. bufo* must have had a pair of subanal tufts of spines.

REMARKS. *Hemiaster bufo* was first described and figured by Brongniart (1822). Although it is a relatively well known species on the continent, it has not previously been reported from Britain. There is a species of *Hemiaster* in the Cenomanian Grey Chalk of Folkstone, *H. morrisii* Forbes, which is much flatter and much less wedge-shaped in profile than *H. bufo*, and has longer petals. It is so different in overall shape that it cannot possibly be confused with *H. bufo*.

Subgenus ***BOLBASTER*** Pomel, 1869

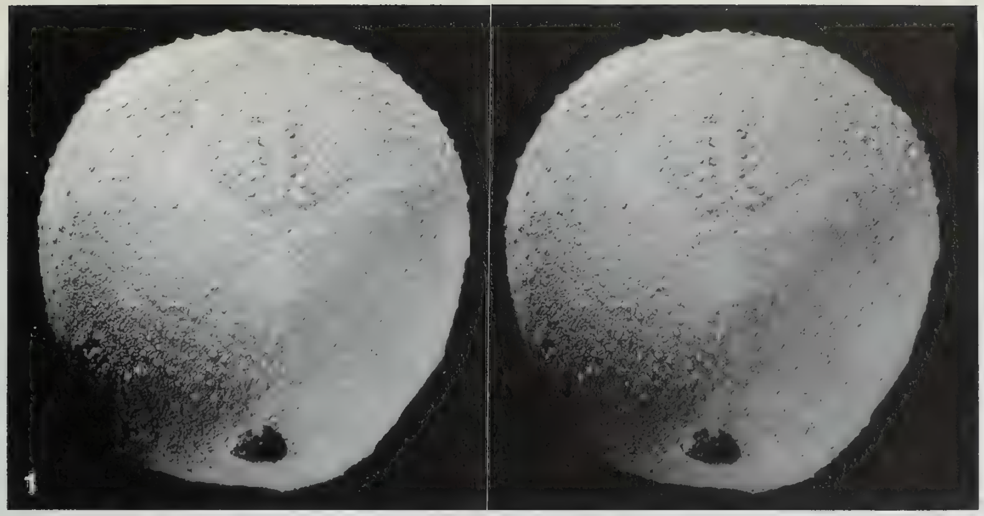
Hemiaster (Bolbaster) nasutulus Sorignet 1850

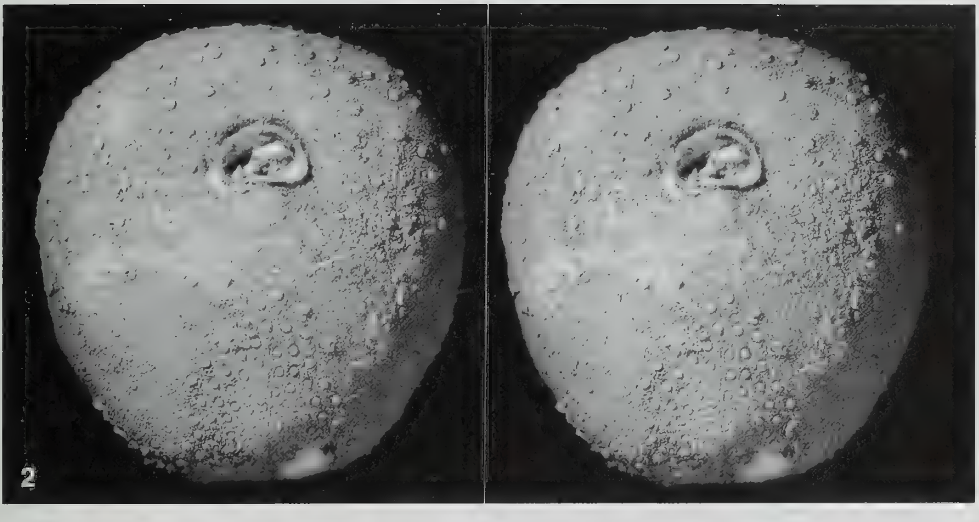
Pl. 37, figs 1–4; Pl. 38, figs 1, 2; Figs 68, 69b, 71

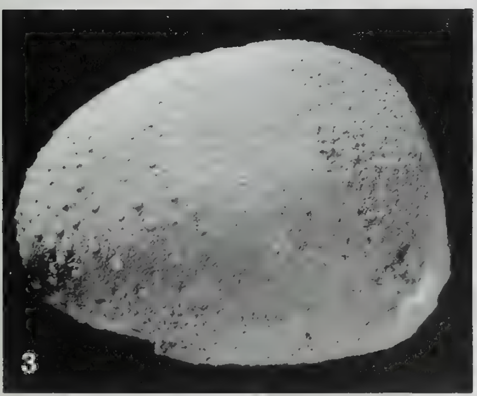
1850 *Hemiaster nasutulus* Sorignet: 53.
1876 *Hemiaster nasutulus* Sorignet; Cotteau: 349; pl. 76, figs 5, 6.
1903 *Hemiaster nasutulus* Sorignet; Lambert: 7.
1924 *Peroniaster nasutulus* (Sorignet) Lambert & Thiéry: 507.

MATERIAL. The following description is based on three specimens (E.80628–9, E.80642) collected at Wilmington. A fourth, damaged specimen (E.80643) was also collected there. A large number of Turonian specimens from south Devon coastal exposures were also examined for comparison.

STRATIGRAPHICAL OCCURRENCE AND DISTRIBUTION. All four specimens from Wilmington are preserved in a glauconitic chalk and must have come from the basal part of the Middle Chalk. The two specimens collected *in situ* come from 10 cm and 18 cm above the datum level at the







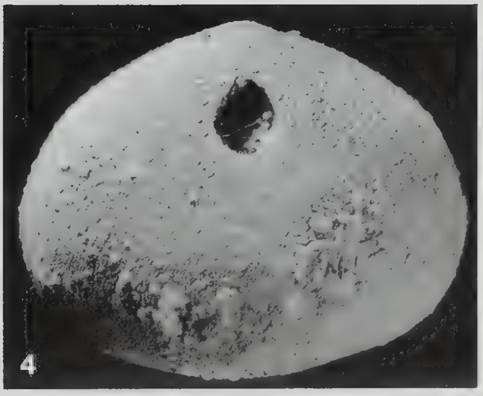


Plate 37
Hemiaster (*Bolbaster*) *nasutulus* Sorignet
Figs 1–4 E.80642: 1, apical; 2, oral; 3, lateral, anterior to left; 4, posterior. Lower Turonian, White Hart sand pit, Wilmington, Devon (× 6). See also Pl. 38, fig. 2.

base of the Middle Chalk. They therefore come from the Lower Turonian. This species is found in Lower Turonian chalk throughout southern England.

DESCRIPTION. *SIZE AND SHAPE.* The three specimens measure 10·4, 13·7 and 16·2 mm in length and this species rarely grows much larger in populations from elsewhere. The test is subspherical with a width 92–99% of the test length (mean = 96%; SD = 3·7; N = 3). In outline the test is roughly egg-shaped with a broad, slightly rounded anterior and a more tapered posterior. The widest point on the test lies 43–46% of the test length from the anterior border (mean = 44%; SD = 2·5; N = 3). There is no frontal sulcus. In profile the test is tall and wedge-shaped. The height of the test is 72–77% of the test length (mean = 75%; SD = 2·5; N = 3) and the highest point lies 66–73% of the test length from the anterior border (mean = 6%; SD = 3·9; N = 3), coinciding with a point midway between the apical disc and the periproct. The test slopes forward to a rounded anterior while the posterior is obliquely truncated so as to form a subanal heel. The base of the test is slightly convex.

APICAL DISC. The apical disc is small and more or less circular in outline. The four gonopores are open, even in the smallest specimen, showing that even at 10·4 mm test length individuals were sexually mature. The four genital plates abut centrally and appear to be broadly similar in size. The hydropores, which total no more than a dozen, are confined to genital plate 2. Ocular plates II, III and IV are relatively large and triangular in outline (Fig. 69b). The posterior pair of ocular plates are not clearly seen in any of the specimens but are presumably in contact. The apical disc lies 52–57% of the test length from the anterior border of the test, and is very slightly sunken.

AMBULACRA. All five ambulacra are feebly sunken adapically. The anterior ambulacrum lies in the broadest and longest adapical depression which extends up to the fasciole (about 60% of the distance to the ambitus). Ambulacral pores within the peripetalous fasciole are large, prominent isopores with a circular attachment rim and a bulbous interporal partition. There are six large isopores per column in the 10·4 mm individual and eight in the 13·7 mm individual. Below this, from just within the fasciole to the phyllode pores adjacent to the peristome, ambulacral pores are minute unipores that are almost impossible to find.

In ambulacra II and IV the adapical sunken zones are long and narrow, extending for 50% of the distance to the ambitus and terminating openly at the fasciole. They are 15–19% of the test length and the width of the sulcus is 22–24% of its length. Ambulacral pores within this zone are minute circumflexed isopores with a narrow, slightly raised interporal partition, and are not conjugate. There are 8 isopores per column at 10·4 mm test length and 11 at 13·7 mm test length. The ambulacra are more or less straight and lie at an angle of 75° to the anterior.

The posterior ambulacra are the most feebly sunken adapically and are also the shortest. The shallow sunken zone extends only 25–30% of the distance to the ambitus and is only 7–10% of the test length in length. Ambulacral pores within this zone are minute isopores like those in the anterior paired ambulacra. There are six isopores per column in the 10·4 mm individual and eight in the 13·7 mm individual. They terminate openly at the fasciole. Pores below the fasciole are minuscule and very difficult to locate.

Immediately adjacent to the peristome there are a small number of large unipores (Pl. 37, fig. 2). These unipores have a large circular periporal zone with a pair of parallel ridges bounding a median groove which leads into the single marginal pore. There are two of these phyllode pores per column in ambulacrum III, three or four in ambulacra II and IV and two in ambulacra I and V.

INTERAMBULACRA. Adapically the posterior interambulacrum is raised to form a low, rounded crest. On the oral surface there are only three plates in each interambulacrum (Fig. 71b). In the posterior interambulacrum, the labral plate is long and narrow with a strongly concave posterior edge. The length of this plate is 20–22% of the test length. Both sternal plates are in contact with the labral plate, but the suture between them is oblique and reaches the labral plate close to the right-hand margin (Fig. 71b).

PERIPROCT. The periproct is small and oval in outline. It is situated high on the posterior face. The height of the periproct opening is 18–21% of the height of the test (mean = 20%;

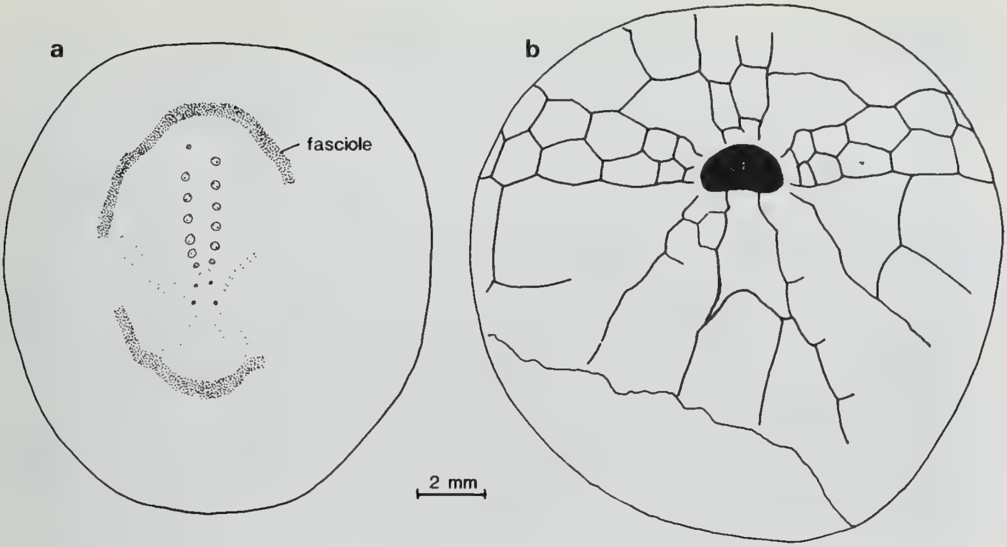


Fig. 71 Camera lucida drawings of *Hemiaster nasutulus* from the Lower Turonian of Wilmington: a, E.80628, adapical surface showing fasciole pattern; b, E.80629, oral plating.

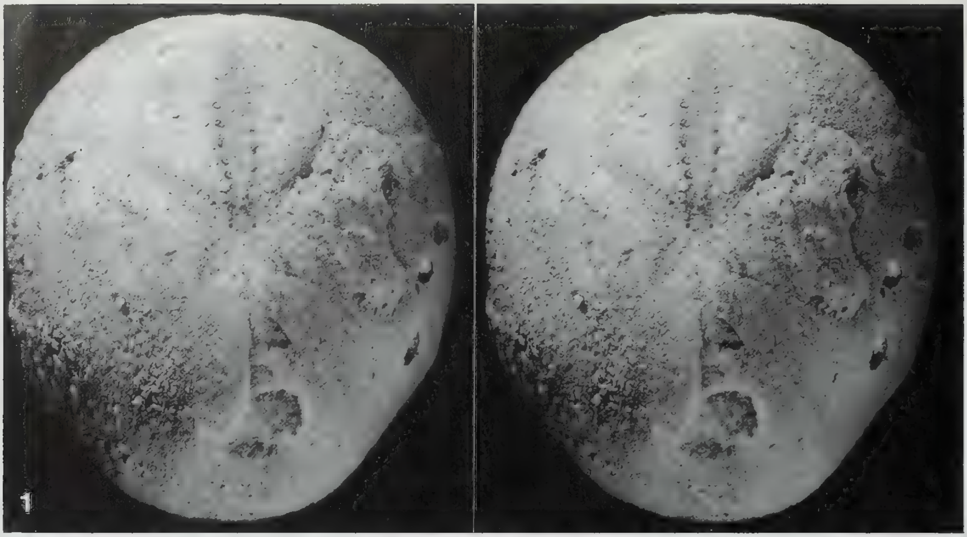
SD = 1·9; N = 3) and its width is 66–76% of its height (mean = 72%; SD = 4·9; N = 3). The base of the periproct lies 60–83% of the test height above the base of the test (60% in the smallest individual, 83% in the largest).

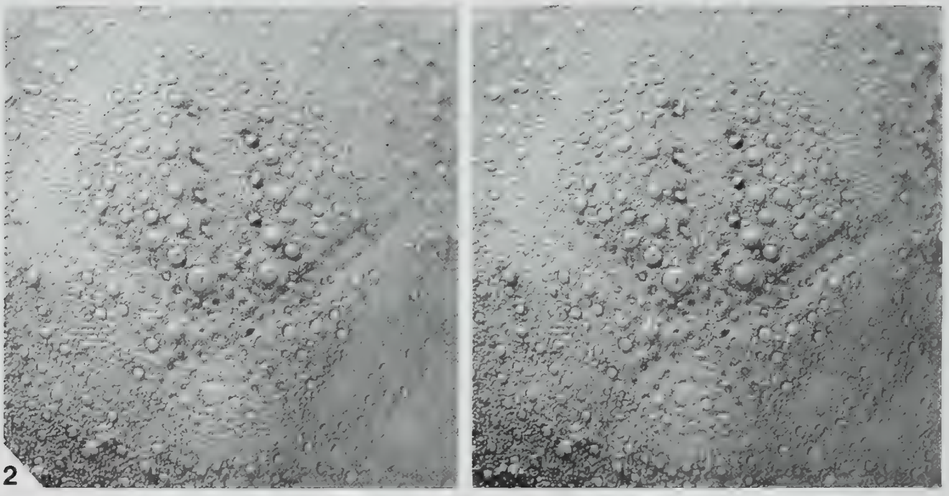
PERISTOME. The peristome is roughly D-shaped in outline, with a convex anterior margin and a straight or very slightly concave posterior face. The length of the peristome is 9% of the test length in all three specimens, while the width of the peristome is 1·8–1·9 times its length. The anterior edge of the peristome lies 23–28% of the test length from the anterior border of the test (mean = 26%; SD = 2·5; N = 3). The peristome is surrounded by a prominent rim and groove.

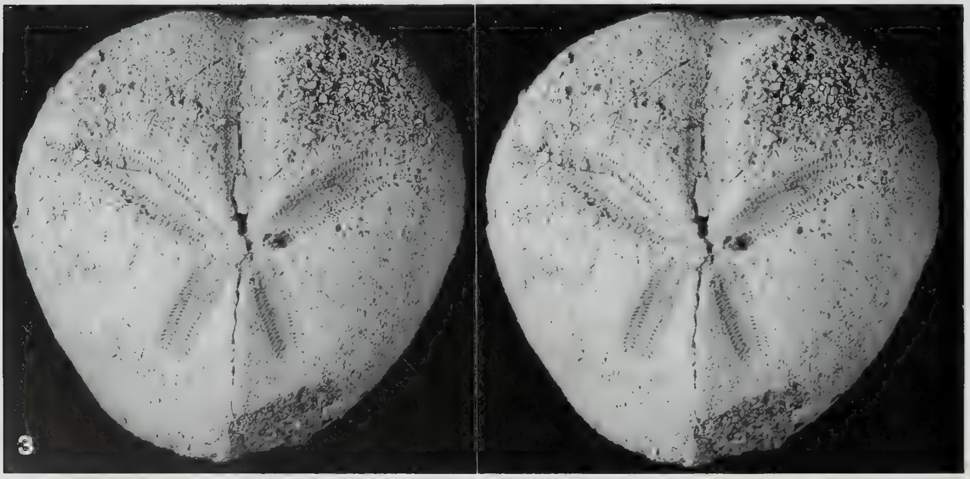
TUBERCULATION. There is a prominent peripetalous fasciole. This is ovoid and slightly angular in outline and is composed of densely-packed miliaries some six or seven abreast. The distance from the anterior to the posterior border of the fasciole measures 53–63% of the test length while its width is 70–80% of its length. Dorsal tubercles on either side of the fasciole are very small and closely packed, measuring little more than 0·1 mm in diameter. Larger tubercles border the shallow adapical sinus within the peripetalous fasciole and these are up to 0·2 mm in diameter. Dorsal tubercles become a little larger and stouter around the anterior ambitus. Tubercles are closely packed on the sternal plates and have areoles that are enlarged towards the posterior. There are no tubercles on the labrum. Tubercles in the lateroventral region are sparse. There is no cluster of tubercles in the subanal region, nor are there any modified ambulacral pores.

REMARKS. This species was first proposed and briefly described by Sorignet (1850) but not figured until Cotteau (1876) restudied it. It was first recorded from the Turonian of south-western England by Lambert (1903).

H. nasutulus is very like juveniles of *H. bufo*, but has gonopores and was sexually mature by a size of 10 mm. *H. nasutulus* clearly represents a paedomorphic species of *Hemiaster*. Small paedomorphic forms of *Hemiaster* are common in the Upper Cretaceous chalk facies of the Anglo-Paris basin and probably represent a natural group. The subgenus *Bolbaster* Pomel, whose type species is *H. prunella* (Lamarck), is the oldest available name for this group.


1


2


3

Species composition and abundance in Units a to j

Unit j Middle Chalk (Turonian, *I. labiatus* Zone) from datum level to 1·5 metres above datum level (phosphatized Upper Cenomanian specimens excluded).

Number of specimens collected = 11

Irregular echinoids (10 specimens) – 91% of the total

Discoides inferus	3
Conulus subrotundus	2
Cardiaster truncatus	2
Hemiaster nasutulus	2
Cardiotaxis cf. *cretacea*	1

Regular echinoids (1 specimen)—9% of the total

Prionocidaris granulostriata	1 (plus spines)

Unit i Wilmington Limestone (Middle Cenomanian, *A. rhotomagense* Zone) from datum level to 80 cm below datum level.

Number of specimens collected = 9

Irregular echinoids (8 specimens)—89% of total

Echinogalerus rostratus	2
Holaster nodulosus	2
Holaster subglobosus	2
Conulus castanea	1
Catopygus columbarius	1

Regular echinoids (1 specimen)—11% of total

Tetragramma variolare subnudum	1

Unit h Grizzle (Lower Cenomanian, *M. dixoni* Subzone) from 81 cm to 145 cm below datum level.

Number of specimens collected = 130

Irregular echinoids (108 specimens)—83% of the total

		as % of irregulars	as % of total
Discoides subuculus	59	56	46
Conulus castanea	15	14	12
Holaster nodulosus	12	11	9
Holaster bischoffi	11	10	9
Echinogalerus rostratus	7	5	4
Catopygus columbarius	3	3	2
Discoides favrinus	1	1	1

Regular echinoids (22 specimens)—17% of total

		as % of regulars	as % of total
Salenia petalifera	4	18	3
Cottaldia benettiae	4	18	3
Goniophorus lunulatus	3	14	2
Polydiadema bonei	3	14	2
Hyposalenia umbrella	2	9	2

Plate 38

Hemiaster (*Bolbaster*) *nasutulus* Sorignet

Fig. 1 E.80628, apical. Lower Turonian, White Hart sand pit, Wilmington, Devon (×5·3).

Fig. 2 E.80642, detail of apical region. As last (×12). See also Pl. 37.

Micraster distinctus Agassiz & Desor

Fig. 3 BGS GSM 108782, apical. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (×1·5).

		as % of regulars	as % of total
Cottaldia granulosa	2	9	2
Stereocidaris essenensis	1	5	1
Tylocidaris velifera	1	5	1
Tetragramma variolare subnudum	1	5	1
Glyptocyphus difficilis	1	5	1

Unit g Grizzle (Lower Cenomanian, *M. mantelli* Zone) from 146 cm to 233 cm below datum level.

Number of specimens collected = 191

Irregular echinoids (148 specimens)—77% of the total

		as % of irregulars	as % of total
Discoides subuculus	54	36	28
Holaster nodulosus	41	28	22
Holaster bischoffi	36	24	19
Echinogalerus rostratus	8	5	4
Catopygus columbarius	9	6	5

Regular echinoids (43 specimens)—23% of the total

		as % of regulars	as % of total
Polydiadema bonei	11	26	6
Hyposalenia clathrata	7	16	4
Tiaromma michelini	5	12	2·5
Tetragramma variolare subnudum	5	12	2·5
Stereocidaris essenensis	4	9	2
Cottaldia granulosa	4	9	2
Goniophorus lunulatus	2	5	1
Glyptocyphus difficilis	2	5	1
Glyphocyphus radiatus	2	5	1
Salenia petalifera	1	2	0·5

Unit f Grizzle (Lower Cenomanian, *M. mantelli* Zone) from 234 cm to 283 cm below datum level.

Number of specimens collected = 189

Irregular echinoids (156 specimens)—82% of the total

		as % of irregulars	as % of total
Holaster nodulosus	64	42	35
Discoides subuculus	52	34	28
Catopygus columbarius	23	15	12
Echinogalerus rostratus	17	11	9

Regular echinoids (33 specimens)—18% of the total

		as % of regulars	as % of total
Polydiadema bonei	17	52	9
Tiaromma michelini	4	12	2
Tetragramma variolare subnudum	3	9	2
Hyposalenia clathrata	3	9	2
Stereocidaris essenensis	2	6	1
Salenia petalifera	2	6	1
Cottaldia granulosa	2	6	1

Unit e Base of Grizzle to top of Wilmington Sands (Lower Cenomanian, *M. mantelli* Zone) from 284 cm to 350 cm below datum level.

Number of specimens collected = 248

Irregular echinoids (225 specimens)—91% of the total

		as % of irregulars	as % of total
Catopygus columbarius	118	53	48
Holaster nodulosus	66	29	27
Discoides subuculus	24	12	10
Echinogalerus rostratus	11	4	4
Labrotaxis tricarinata	3	1·5	1
Hemiaster bufo	2	1	1
Micraster distinctus	1	0·5	—

Regular echinoids (23 specimens)—9% of the total

		as % of regulars	as % of total
Tiaromma michelini	6	26	3
Polydiadema bonei	3	13	1
Tetragramma variolare subnudum	3	13	1
Cottaldia granulosa	3	13	1
Stereocidaris essenensis	3	13	1
Goniophorus lunulatus	2	9	1
Salenia petalifera	1	4	—
Allomma rhodani	1	4	—
Glyptocyphus difficilis	1	4	—

Unit d Wilmington Sands (Lower Cenomanian, *M. mantelli* Zone) from 351 cm to 500 cm below datum level.

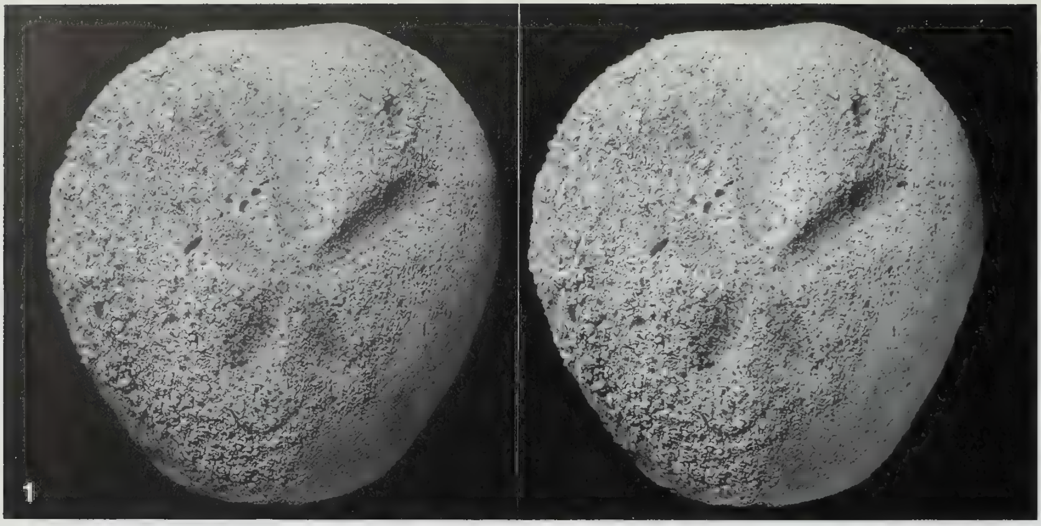
Number of specimens collected = 329

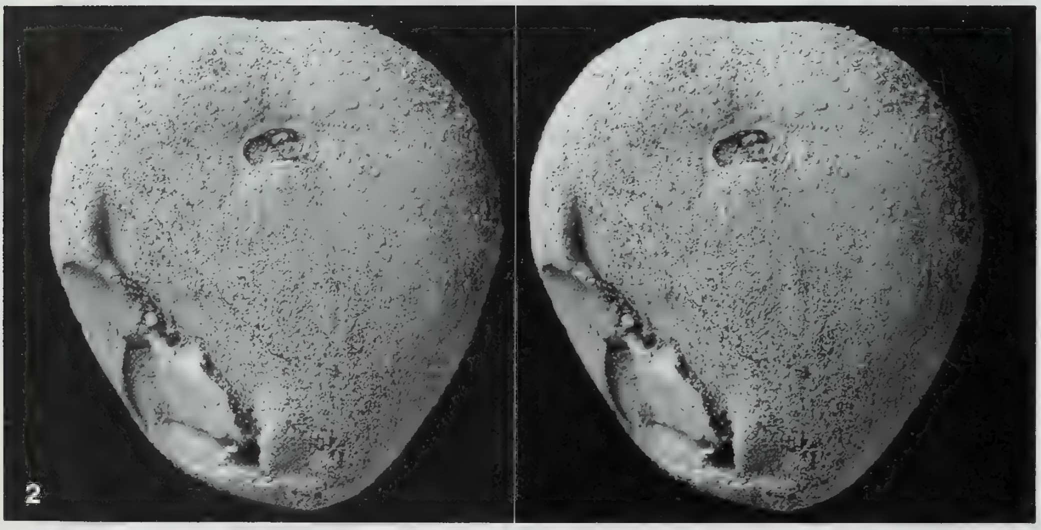
Irregular echinoids (266 specimens)—81% of the total

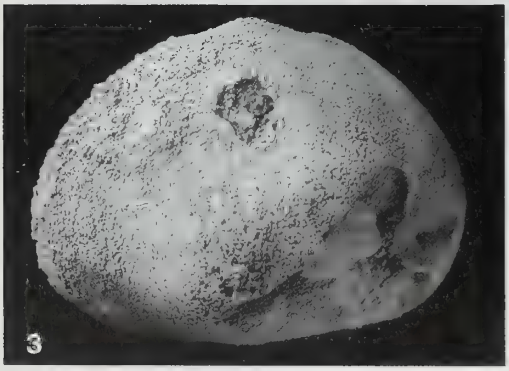
		as % of irregulars	as % of total
Holaster nodulosus	118	45	36
Echinogalerus rostratus	56	21	17
Discoides subuculus	53	20	16
Catopygus columbarius	32	12	10
Hemiaster bufo	3	1	1
Labrotaxis tricarinata	3	1	1
Holaster bischoffi	1	—	—

Regular echinoids (63 specimens)—19% of the total

		as % of regulars	as % of total
Tetragramma variolare subnudum	23	37	7
Tiaromma michelini	15	24	5
Polydiadema bonei	9	14	3
Glyphocyphus radiatus	6	10	2
Stereocidaris essenensis	3	5	1
Salenia petalifera	3	5	1
Cottaldia granulosa	2	3	1
Allomma rhodani	1	2	—
Glyptocyphus difficilis	1	2	—







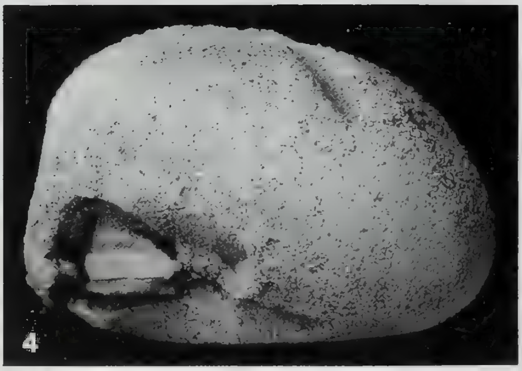


Plate 39

Micraster distinctus Agassiz & Desor

Figs 1–4 E.80625: 1, apical; 2, oral; 3, lateral, anterior to left; 4, posterior. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 1·5).

Unit c Wilmington Sands (Lower Cenomanian, *M. mantelli* Zone) from 501 cm to 650 cm below datum level.

Number of specimens collected = 233

Irregular echinoids (194 specimens)—83% of the total

		as % of irregulars	as % of total
Discoides subuculus	82	44	36
Echinogalerus rostratus	57	29	24
Holaster nodulosus	48	26	21
Catopygus columbarius	7	4	3

Regular echinoids (39 specimens)—17% of the total

		as % of regulars	as % of total
Tetragramma variolare subnudum	14	36	6
Stereocidaris essenensis	6	15	3
Polydiadema bonei	6	15	3
Salenia petalifera	3	8	1
Tiaromma michelini	3	8	1
Goniophorus lunulatus	2	5	1
Allomma rhodani	2	5	1
Glyphocyphus radiatus	2	5	1
Cottaldia benettiae	1	3	—

Unit b Basal part of Wilmington Sands (Lower Cenomanian, *M. mantelli* Zone) from 651 cm to 940 cm below datum level.

Number of specimens collected = 138

Irregular echinoids (119 specimens)—86% of the total

		as % of irregulars	as % of total
Discoides subuculus	57	48	42
Echinogalerus rostratus	32	27	23
Catopygus columbarius	16	14	12
Holaster nodulosus	7	6	5
Echinogalerus faba	5	4	4
Hemiaster bufo	1	1	1
Labrotaxis tricarinata	1	1	1

Regular echinoids (19 specimens)—14% of the total

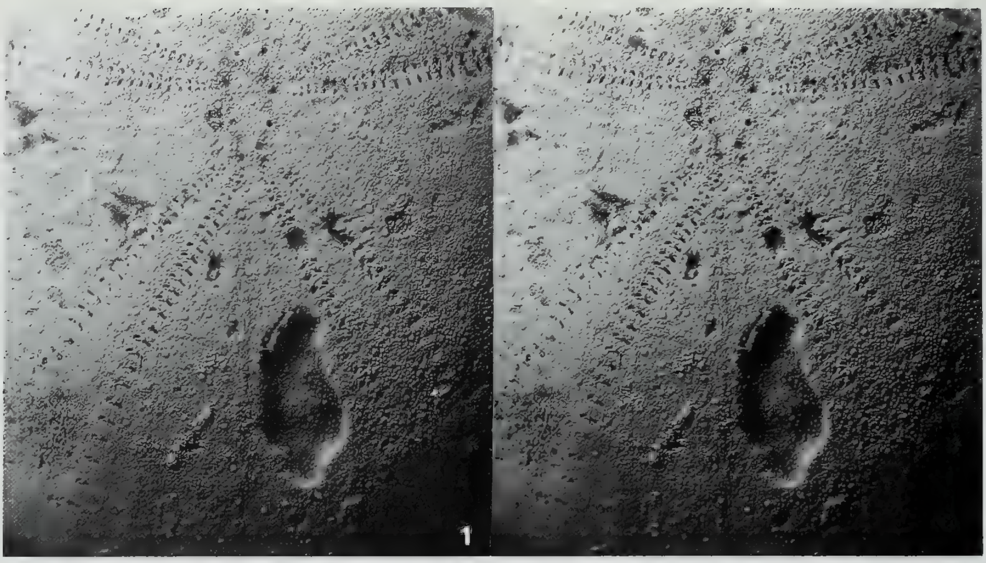
		as % of regulars	as % of total
Stereocidaris essenensis	7	37	5
Tetragramma variolare subnudum	4	21	3
Hyposalenia umbrella	2	11	2
Polydiadema bonei	2	11	2
Salenia petalifera	1	5	1
Tiaromma michelini	1	5	1
Cottaldia benettiae	1	5	1
Glyptocyphus difficilis	1	5	1

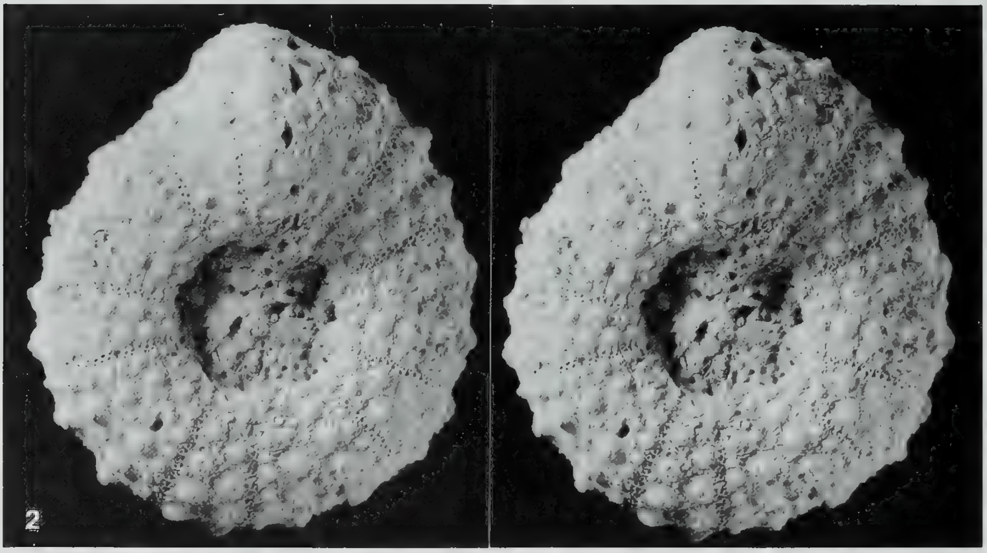
Unit a 'Upper Greensand' (Lower Cenomanian, *M. saxbii* Subzone) from 941 cm downwards.

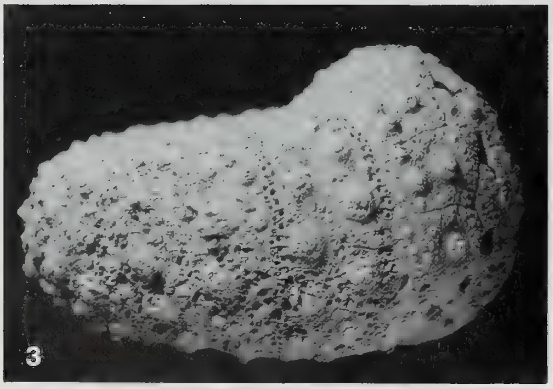
Number of specimens collected = 35

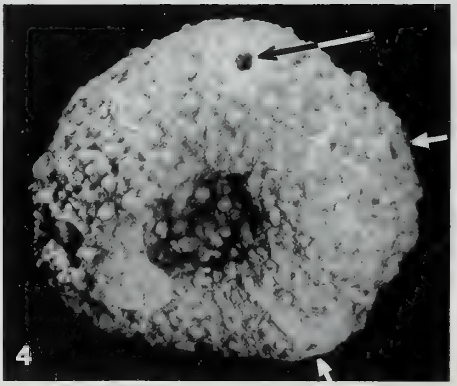
Irregular echinoids (33 specimens)—94% of the total

		as % of irregulars	as % of total
Discoides subuculus	11	33	31
Catopygus columbarius	8	24	23
Echinogalerus rostratus	6	18	17


1


2


3


4

		as % of irregulars	as % of total
Echinogalerus faba	3	9	9
Labrotaxis cenomanensis	2	6	6
Ochetes cf. *placentula*	1	3	3
Holaster revestensis	1	3	3
Holaster laevis	1	3	3

Regular echinoids (2 specimens)—6% of the total

		as % of total
Stereocidaris essenensis	1	3
Polydiadema bonei	1	3

Asteroids

by A. S. Gale

Introduction

In the White Hart pit at Wilmington, asteroids occur only as dissociated ossicles. These are found frequently, but the majority are in a poor state of preservation, owing particularly to superficial pitting by sand grains; consequently, 30–40% of those collected are indeterminate.

Dissociated asteroid ossicles may be identified to the level of genus and species by reference to more complete specimens. In his description of Cretaceous asteroids from north-west Europe, Spencer (1905, 1913) related fossil asteroid ossicles to particular species by this means. This is relatively easy in low energy, fine-grained deposits like the Chalk, in which associated remains of individuals, or even whole specimens, are to be found. In the Cenomanian sands and sandy limestones of south-west England and north-west France, however, high-energy conditions of deposition meant that asteroid skeletons were rapidly dispersed after death. Thus, few endemic taxa are known from well-preserved individuals. However, several well-preserved individuals of the genus *Mastaster* are known from Normandy (Mercier 1935, Breton 1979).

The only previous records of asteroids from Wilmington were made by Wright & Wright (1940), who mentioned three species from the Cenomanian; *Calliderma* (*Mastaster*) *villersensis* Mercier, *Metopaster thoracifer* (Geinitz) and *Metopaster* sp.

The present study is based on 130 ossicles collected *in situ* (Fig. 72), and approximately 1100 collected loose from spoil heaps. This material demonstrates the existence of a highly diverse asteroid fauna comprising 18 species. However, many of these species are represented by only a few ossicles and so cannot be described in detail. Some of the species which occur at Wilmington are also known from the Devon coast, and several have been collected in the Rye Hill Sands of the Warminster district (Wiltshire).

Plate 40

Holaster subglobosus (Leske)

Fig. 1 E.80284, adapical part of interambulacrum 5 showing an irregular, depressed zone of regenerated and repaired plating, presumably the result of predation. Middle Cenomanian, White Hart sand pit, Wilmington, Devon (× 4).

Polydiadema bonei (Woodward)

Figs 2, 3 E.81330, parasitized specimen; 2, apical; 3, lateral. One interambulacrum is greatly swollen and has developed sutural gaps between plates as a result of parasitization. Lower Cenomanian, White Hart sand pit, Wilmington, Devon (× 3·5).

Glyphocyphus radiatus (Agassiz)

Fig. 4 E.81328, parasitized specimen, oral view. Three circular bore holes penetrate the test (arrowed), causing the surrounding area to become swollen. As last (× 4·5).

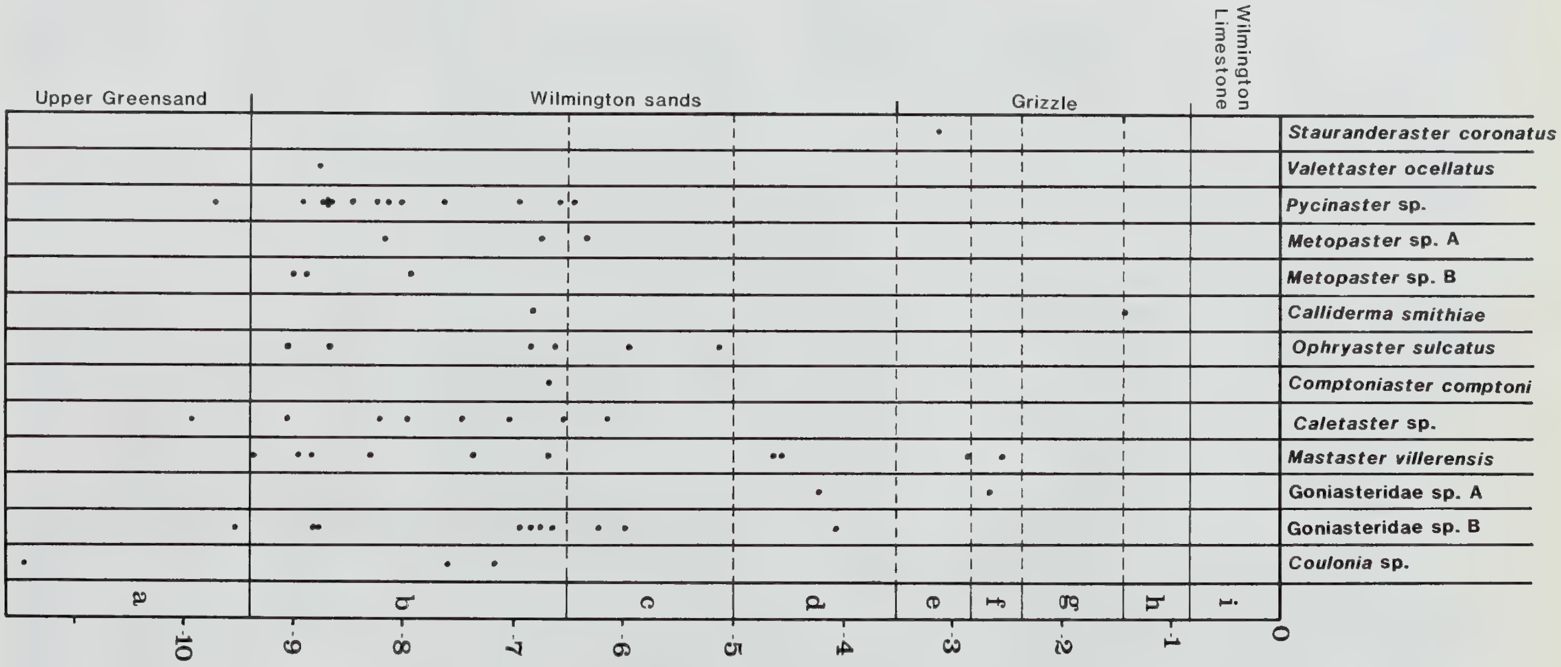


Fig. 72 Stratigraphical distribution of asteroid species within the succession at the White Hart pit, Wilmington. Each dot represents a single specimen located accurately within the succession and plotted against the composite section (see Fig. 4, p. 8).

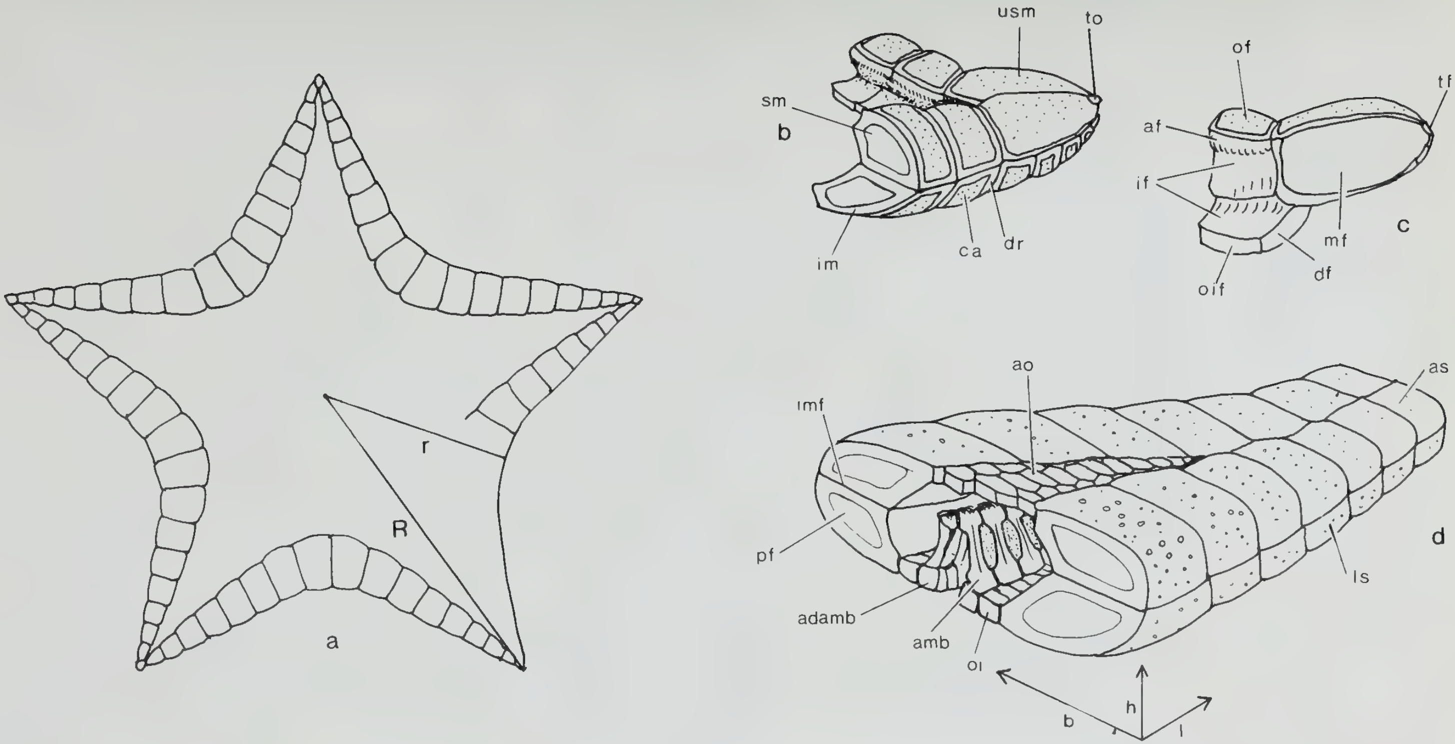


Fig. 73 Ossicle terminology applied to goniasterid starfish in this paper. a, aboral surface of a generalized goniasterid. b, single radius (marginal ossicles only) of the genus *Metopaster*. c, internal view of distal radius of *Metopaster*. d, fragment radius of longer-armed goniasterid *Calliderma*. Abbreviations: adamb = adambulacral ossicle; af = aboral facet; amb = ambulacral ossicle; ao = aboral ossicles; as = aboral surface; b = breadth; ca = central area; df = distal facet; dr = depressed rim; h = height; if = internal face; im = inferomarginal; imf = intermarginal facet; l = length; ls = lateral surface; mf = median facet; of = outer face; oi = oral intermediate ossicle; oif = oral intermediate facet; pf = proximal facet; r = minor radius; R = major radius; sm = superomarginal ossicle; tf = terminal facet; usm = ultimate superomarginal.

The Wilmington asteroid fauna, in common with most of the marine Cretaceous of north-west Europe, is dominated by the Goniasteridae, to which twelve of the species recorded in this paper belong. Modern representatives of the family are notoriously varied in their preferences of substrate and diet. For example, the extant species *Mediaster aequalis* Stimpson is known to deposit-feed on sediment, suspension-feed, predate small benthonic organisms and scavenge (Mauzey *et al.* 1968). In contrast, *Hippasteria spinosa* Verrill lives solely on the pennatulid *Ptilosarcus*. There is little known about the detailed relationships between life habit and skeletal morphology of most extant asteroids, and interpretation of the functional morphology of fossil species is thus possible only by inference. No attempt is made here to describe the autecology of the Wilmington fauna.

Terms used to describe asteroid ossicles in this section are given in Fig. 73. The most important single source of this terminology is Müller (1953), but Rasmussen (1950), Spencer & Wright (1966) and Blake (1973) all provide useful summaries and discussions of previous usages. Detailed morphological terms are provided only for marginal ossicles since species descriptions are almost exclusively concerned with these. Several points need discussion here. It is necessary to emphasize that the terms 'length', 'height' and 'breadth' of ossicles are used only in the same sense as they are in the entire arm. Additionally, I follow Müller (1953) in using the term 'facet' for any articulation surface (as in common English usage) and reserve 'face' for surfaces which are not in contact with other ossicles.

The term 'lateral' is used with reference to the margin, in oral or aboral aspect, of the disc and arms; thus, the 'lateral margin' of a marginal ossicle is that furthest away from the mid-radial line.

Systematic descriptions

The species of asteroids described in this paper are classified as follows.

Order Valvatida Perrier 193
  Family Stauranderasteridae Spencer 193
    Genus *Aspidaster* de Loriol 193
      Aspidaster sp. 193
    Genus *Stauranderaster* Spencer 193
      Stauranderaster coronatus (Forbes) 193
  Family Sphaerasteridae Schöndorf 194
    Genus *Valettaster* Lambert 194
      Valettaster ocellatus (Forbes) 194
  Family Pycinasteridae Spencer & Wright 195
    Genus *Pycinaster* Spencer 195
      Pycinaster sp. 195
    Genus *Phocidaster* Spencer 197
      Phocidaster grandis Spencer 197
  Family Goniasteridae, Subfamily Goniasterinae Forbes 198
    Genus *Metopaster* Sladen 198
      Metopaster sp. A 198
      Metopaster sp. B 199
      Metopaster sp. C 199
  Family Goniasteridae Forbes, Subfamily uncertain 199
    Genus *Calliderma* Gray 199
      Calliderma smithiae (Forbes) 199
    Genus *Ophryaster* Spencer 200
      Ophryaster sulcatus (Sladen) 200
    Genus *Comptoniaster* Breton 202
      Comptoniaster comptoni (Forbes) 202
    Genus *Caletaster* Breton 202
      Caletaster sp. 202
    Genus *Crateraster* Spencer 203
      Crateraster quinqueloba (Goldfuss) 203

Genus *Mastaster* Mercier 203
Mastaster villersensis Mercier 203
Mastaster sp. 204

Goniasteridae species A 205
Goniasteridae species B 205
Order Paxillosida Perrier 207
Family Astropectinidae Gray 207
Genus *Coulonia* de Loriol 207
Coulonia sp. 207

Order **VALVATIDA** Perrier, 1884

Family **STAURANDERASTERIDAE** Spencer, 1913

DIAGNOSIS. Valvatida in which the domed aboral surface of the large disc bears conspicuous tumid primary interradial and central ossicles. The margins of all the aboral ossicles and marginals are notched for papulae.

Genus ***ASPIDASTER*** de Loriol, 1884

TYPE SPECIES. *Aspidaster delgadoi* de Loriol, 1884, by original designation.

Aspidaster sp.

MATERIAL. A single large aboral ossicle from the disc, probably a primary interradial, collected loose in the White Hart pit (E.54033).

DESCRIPTION. In aboral aspect, the ossicle is teardrop-shaped and nearly twice as long as broad. The outer face is tumid and is evenly covered by large, widely spaced granule pits. At the narrow end, the margin is notched on either side. The inner surface bears a ridge along the length of the ossicle, separating two discrete facets.

The shape, and the tumid outer face bearing large granule pits and lacking a depressed border, are characteristic of the genus *Aspidaster*. Comparison with well-preserved individuals of *A. bulbiferus* (Forbes) from the late Coniacian or Santonian Chalk (*coranguinum* Zone) of south-east England (e.g. specimen 48748, from 'Bromley, Kent') allows identification of the ossicle as a primary interradial.

Genus ***STAURANDERASTER*** Spencer, 1907

TYPE SPECIES. *Oreaster boysii* Forbes, 1848, by original designation.

Stauranderaster coronatus (Forbes 1848)
Pl. 41, fig. 2

HOLOTYPE. The specimen figured by Forbes, *in* Dixon 1850: pl. 21, fig. 7; BMNH 35480. Lower Chalk (Cenomanian) of Washington, Sussex.

MATERIAL. A single well-preserved proximal inferomarginal ossicle (E.54031; Pl. 41, fig. 2) was collected *in situ* in the lower part of the Grizzle (3·13 m below datum) in the White Hart pit (Fig. 72). Two inferomarginal ossicles and two aboral ossicles from the disc were found loose (E.54032).

DESCRIPTION. The proximal inferomarginal ossicle E.54031 is taller than broad. In lateral aspect (Pl. 41, fig. 2b) the proximal and distal margins are parallel-sided; the distal margin is concave, the proximal convex. Aborally, the proximal margin is notched. The outer face is evenly curved and bears a narrow, depressed rim. The raised central area is smooth, lacking granule pits, and a single winged pedicellaria (alar type of Schulz & Weitschat, 1971) is present on the upper part. Both proximal and distal facets are concave and bear small rounded protuberances (Pl. 41, fig. 2a).

Remarks. *S. coronatus* is known from several well-preserved individuals from the Lower Chalk (Cenomanian) of south-east England. The holotype 35480 is an incomplete disc and proximal part of one arm. A nearly entire individual from the Lower Chalk of Burham, Kent (E.2562) was figured by Spencer (1905: pl. 19, fig. 1). A third specimen, which probably came from the Lower Chalk between Dover and Folkestone, is in the British Geological Survey collection (GSM 108658).

Comparison of the well-preserved Wilmington ossicle E.54031 with the holotype of *S. coronatus* indicates that it is the 3rd or 4th interradial inferomarginal (shape, height : length ratio, size of outer face). The presence of a single, wing-shaped pedicellaria is characteristic of the species.

Occurrence. *S. coronatus* is an uncommon species which is found in the Cenomanian of southern England, in both the basinal marly chalk facies and in the marginal sands and sandy limestones. Spencer's records of the species from as late as the *coranguinum* Zone Chalk (late Coniacian or Santonian) are perhaps erroneous (Spencer 1913: 168–169).

Family **SPHAERASTERIDAE** Schöndorf, 1906

Diagnosis. Adorally domed or spherical Valvatida in which arms are absent. The surface is completely covered by a close-fitting tessellation of ossicles.

Genus ***VALETTASTER*** Lambert, 1914

[= *Tholaster* Spencer 1913 *non* Seunes 1890; *Tholasterina* Valette 1915]

Type species. *Oreaster ocellatus* Forbes, 1848, by subsequent designation of Rasmussen (1950).

Remarks. This is not the *Valettaster* of Lambert & Thiéry (1924, **6–7**: 405), a name replaced by *Aurelianaster* Lambert & Thiéry (*loc. cit.*: 589).

Valettaster ocellatus (Forbes 1848)

Pl. 41, fig. 1

Holotype. The cluster of large, disarticulated aboral ossicles, originating in one individual, figured by Forbes (*in* Dixon 1850: pl. 11, fig. 13) is the holotype. Upper Chalk, almost certainly Santonian.

Material. A single large aboral ossicle E.54035 was collected *in situ* near the base of the Wilmington Sands (8·8 m below datum) in the White Hart pit (Fig. 72). In the collection of C. W. & E. V. Wright there are four additional, dissociated aboral ossicles collected loose in both Hutchin's pit and the White Hart pit (WW 12182, 2506). Eight aboral ossicles were collected loose in the White Hart pit (E.54034).

Description. Only the large aboral ossicles of this species are known from Wilmington. These have the form of low, truncated cones (Pl. 41, fig. 1) which in aboral aspect are equidimensional or elongated; the outline of these is irregularly polygonal (Pl. 41, fig. 1a). The interior face is flat or weakly convex. The sloping sides bear irregularly placed, discontinuous radiating ridges separated by grooves. The outer face of the aboral ossicles is flat, proportionately small (Pl. 41, fig. 1b)—about one-third of the maximum dimension—and parallel to the inner face. When well preserved (as the ossicle figured here) the outer face bears an intricate pattern of very fine ridges. These most commonly radiate from the central point or axis, but may be parallel to one of the sides.

Remarks. Ossicles of *Valettaster ocellatus* are common in the White Chalk facies (Turonian to Maastrichtian) of north-west Europe. However, few individuals in which the ossicles are preserved in place are known. The best specimen, BMNH E.5012, is from the *Marsupites* Zone (Santonian) of Brighton, and was figured by Spencer (1905: pl. 25, fig. 4). On the oral aspect of this specimen two ambulacral grooves and the intervening aboral ossicles are visible. In life, the interstices between individual aboral ossicles were packed with smaller plates in such a way that the surface of the asteroid was flat. This is particularly well displayed in a specimen of *Valettaster argus* (Spencer) from the *coranguinum* Zone (Santonian) of Kent (British Geological Survey collection Yd 4806).

OCCURRENCE. The eight ossicles collected loose (E.54034) all originated from the lower part of the succession in the White Hart pit. *V. ocellatus* is found in marginal Cenomanian deposits in south-west England, and Turonian to Maastrichtian Chalk in England, France and Denmark. It also occurs in the Palaeocene (Danian) of Denmark.

Family **PYCINASTERIDAE** Spencer & Wright, 1966

DIAGNOSIS. The marginal ossicles are stout and tall. Only the first-formed pairs of marginals (SM1, IM1) oppose; more distally, supero- and inferomarginals alternate. The marginal ossicles are notched at the intermarginal junction. A large, orally directed dagger-shaped or spatulate spine is present in each interradial area immediately adjacent to the mouth frame.

REMARKS. The above characters of the marginal ossicles and the presence of large oral spines are sufficiently distinctive to merit separation of these asteroids as a discrete family rather than as a subfamily of the Goniasteridae. Two genera were included in the Pycinasterinae by Spencer & Wright (1966); *Pycinaster* and *?Phocidaster*.

Pycinaster is a common genus in the Turonian–Maastrichtian white chalk facies of western Europe and is best known from well-preserved specimens of the type species *P. angustatus* (Forbes) of Santonian age collected in south-east England (e.g. E.20293 from Micheldever, Hants.). Three species of *Pycinaster* were described from the Jurassic of the Paris Basin by Mercier (1935), and the genus is also known from the Palaeocene (Danian) of Denmark (Rasmussen 1950) and the Eocene and Miocene of France (Valette 1925).

Phocidaster is represented by a single species, *P. grandis* Spencer. This is poorly known from a total of 9 large interradial marginals, all dissociated, collected in the Cenomanian of south-west England. These compare with *Pycinaster* in their tall, narrow form, the bulbous aboral region, and the vertical aboral facet and internal face.

Genus ***PYCINASTER*** Spencer, 1907

TYPE SPECIES. *Goniaster* (*Goniodiscus*) *angustatus* Forbes, 1848, by original designation.

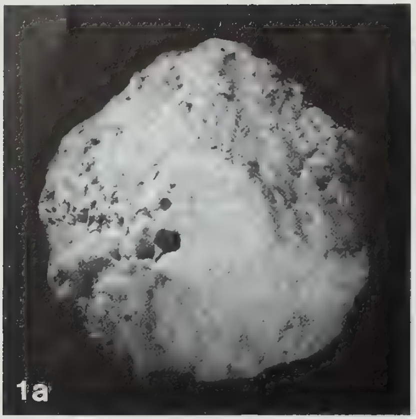
Pycinaster sp.

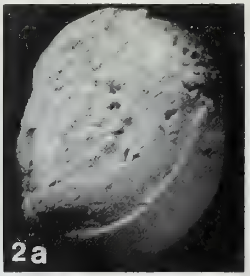
Pl. 41, fig. 3

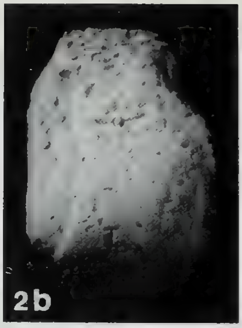
MATERIAL. Eighteen dissociated marginal ossicles have been collected *in situ* in the White Hart pit, Wilmington (E.54036–53): these occur in the lower part of the Wilmington Sands, from 6·47–9·75 m below datum (Fig. 72). Six unregistered marginal ossicles from Wilmington are present in the Wrights' collection. About 200 additional ossicles, collected loose in the White Hart pit, are also available (E.54054).

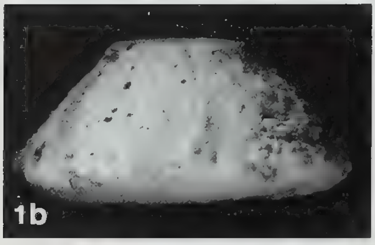
DESCRIPTION. The species is most commonly represented by the conspicuously large interradial superomarginals (E.54036; Pl. 41, fig. 3). These are proportionately tall, as broad as long, and in lateral aspect (Pl. 41, fig. 3a) taper sharply towards the intermarginal facet. The lateral margin is vertical and swollen at the contact with the narrow aboral surface. In some interradial superomarginals the lower part of the lateral surface is concave. Proximal and distal facets of the superomarginals are concave. A narrow articulation ridge runs vertically along the lateral border of each facet. Both proximal (Pl. 41, fig. 3b) and distal borders of each ossicle are notched immediately above the narrow intermarginal facet. The aboral facet is deep.

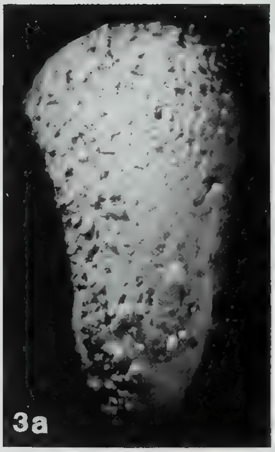
The distal superomarginals are proportionately low, and have well demarcated aboral and lateral surfaces. The inferomarginals are rectangular in profile, short with discrete oral and lateral surfaces. The outer faces of all marginal ossicles are devoid of granule pits and appear smooth.

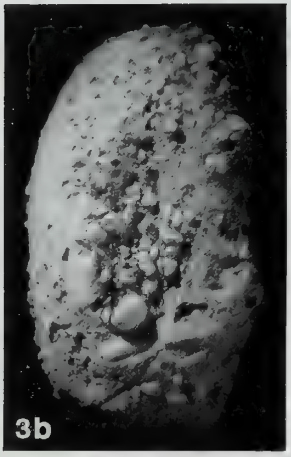

1a

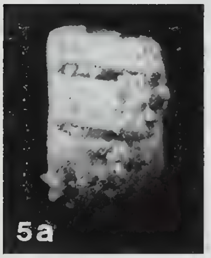

2a

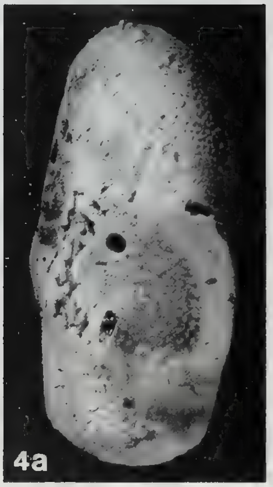

2b

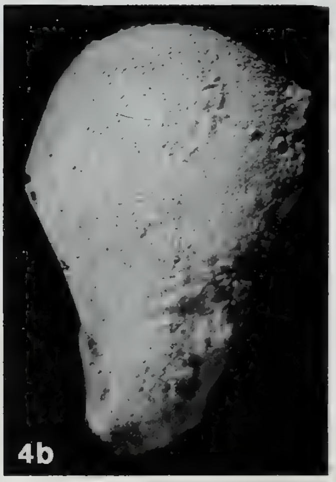

1b

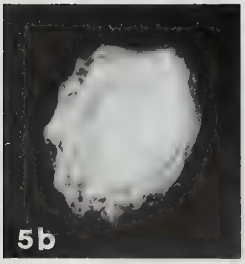

3a


3b


5a


4a


4b


5b

REMARKS. The Wilmington *Pycinaster* does not compare closely with any of the described species of the genus. The only other Cenomanian species which has been described is *P. humilis* Spencer, 1913, the holotype of which (Rowe collection, BMNH E.20952) is from the Chalk Marl of Dover. This consists of an arm fragment and a row of interradial inferomarginals. The distal marginals are as tall as long and have evenly swollen outer faces which bear fine shallow granule pits. A large single alveolar pedicellaria is present on the centre of the lateral surface of each marginal. The Wilmington ossicles differ from those visible in this specimen in that both pedicellariae and granule pits are lacking entirely, and in their broader, shorter interradial inferomarginals. *P. crassus* Spencer from the Coniacian and Santonian Chalk of the Anglo-Paris Basin is distinguished by the presence of pustule-like swellings on the distal marginals.

Genus ***PHOCIDASTER*** Spencer, 1913

TYPE SPECIES. *P. grandis* Spencer, 1913, by original designation.

REMARKS. This genus was described on the basis of large, bulbous interradial superomarginals which Wright & Wright (1940) thought were probably unpaired ossicles prominently positioned in each interradius. These ossicles are not bilaterally symmetrical, but have taller proximal facets than distal ones. Thus, they represent paired interradial superomarginals (SM1) such as are present in *Pycinaster*.

Phocidaster grandis Spencer 1913
Pl. 41, fig. 4

LECTOTYPE. The interradial superomarginal figured by Spencer (1913: pl. 13, fig. 29), herein selected. Rye Hill Sands of the Warminster district (BGS GSM 26694).

MATERIAL. Two interradial superomarginals, collected loose. One in the Wrights' collection, WW 24631, is from 'Wilmington pit 2'; the other (E.54055) is from the White Hart pit.

DESCRIPTION. The well-preserved interradial superomarginal (Pl. 41, fig. 4) is tall and narrow, and swollen aborally. In lateral aspect, the ossicle tapers sharply towards the intermarginal contact. The lateral face is vertical and gently convex, the aboral surface narrow and low. The concave proximal and distal (Pl. 41, fig. 4a) facets extend for approximately two-thirds the total height of the ossicle and bear coarse rugosities. A well-marked, smooth, narrow ridge is present on the lateral border of these facets. The proximal and distal margins are slightly notched immediately above the intermarginal border. The narrow intermarginal facet is made up of two small, oval facets, each of which would have contacted an inferomarginal. The aboral facet is

---

Plate 41

Valletaster ocellatus (Forbes)

Fig. 1 C. W. Wright colln no. 2506, aboral ossicle in aboral aspect (1a) and profile (1b). Cenomanian, Wilmington pit II (× 4·8).

Stauranderaster coronatus (Forbes)

Fig. 2 E.54031, interradial inferomarginal ossicle (im 3 or 4) in distal profile (2a) and lateral view (2b). Grizzle, 3·13 m below datum level, White Hart pit, Wilmington (× 5).

Pycinaster sp.

Fig. 3 E.54034, interradial superomarginal ossicle in lateral (3a) and proximal view (3b). Lower part of the Wilmington Sands, 8·70 m below datum level, White Hart pit, Wilmington (× 4·5).

Phocidaster grandis Spencer

Fig. 4 C. W. Wright colln no. 24631, interradial superomarginal (sm 2 or 3) in distal (4a) and lateral view (4b). Cenomanian, Wilmington pit II (× 4·5).

Comptoniaster comptoni (Forbes)

Fig. 5 E.54081, distal inferomarginal in lateral (5a) and proximal view (5b). Wilmington Sands, 6·71 m below datum level, White Hart pit, Wilmington (× 5·3).

deep and vertical, and bears ridges which would have been in contact with several aboral ossicles.

The outer face (Pl. 41, fig. 4b) of both ossicles bears fine, closely spaced rugosities, between which granules would have been positioned. Near the intermarginal contact, rather large granule pits are present.

REMARKS. The two ossicles from Wilmington are not first-formed interradial superomarginals (SM1); each articulated with two inferomarginals in an alternate arrangement as in *Pycinaster* (see above). The distinctive ornament of fine rugosities compares closely with typical SM1 of *P. grandis*. The ossicles from Wilmington are perhaps the second or third superomarginals (SM2–3) of this species.

OCCURRENCE. *P. grandis* is present in the Rye Hill Sands (Cenomanian) of the Warminster district, Wiltshire (5 ossicles). The matrix on these specimens indicates they came from a horizon within the body of the sands rather than from the basal bed (C. J. Wood, personal communication). Additional specimens are from the Glauconitic Marl (early Cenomanian) of Rocken End, Isle of Wight (1), The Blackdown Greensand (late Albian) of Blackdown, Devon (1) and from Wilmington (2).

Family **GONIASTERIDAE** Forbes, 1841

DIAGNOSIS. The body is flat, although the distal arms may be recurved aborally. The disc is proportionately large. The large and prominent infero- and superomarginals oppose each other. The aboral surface is flat, and covered by a tesselation of tabular to paxilliform small plates.

Subfamily **GONIASTERINAE** Forbes, 1841

DIAGNOSIS. Goniasteridae in which a raised central area is present on the marginal ossicles, and less commonly, on the aboral and oral intermediate ossicles. Enlarged ultimate (or penultimate) superomarginals present.

Genus ***METOPASTER*** Sladen, 1893

TYPE SPECIES. *Goniaster* (*Goniodiscus*) *parkinsoni* Forbes, 1848, by subsequent designation of Rasmussen, 1950.

REMARKS. Several species of the common Upper Cretaceous genus *Metopaster* are present in the White Hart pit at Wilmington. These are each represented by a few, rather badly preserved marginal ossicles. They have been described (Gale 1987) since this paper was submitted.

Metopaster sp. A
Pl. 42, fig. 2

MATERIAL. Three dissociated ultimate superomarginals from Wilmington, in the collection of C. W. & E. V. Wright (WW 16571), recorded and one figured by them (1940: 238; fig. 9a, b, c). A fragmentary ossicle recorded by Wright & Wright (*loc. cit.*) as *M. thoracifer* also probably belongs to this species (WW 12153). There is also a single median marginal from Wilmington 2 (WW 21031) in the same collection. Other specimens: four marginals collected *in situ* in the lower part of the Wilmington Sands (6·35–8·20 m below datum, Fig. 72; E.54058–60), and 14 dissociated ultimate superomarginals and three median marginals collected loose in the White Hart pit (E.54056–7).

DESCRIPTION. The ultimate superomarginal ossicles are as broad as high and twice as long (Pl. 42, fig. 2), and taper distally. The outer face (Pl. 42, fig. 2a) is evenly curved and bears shallow granule pits, separated by rugosities. On one ossicle the rugosities are seen to be coarse and elongated. There is no discrete central area and border. The proximal facet (Pl. 42, fig. 2b) is weakly concave and set at right angles to the long, flat, triangular median facet. Three or four inferomarginals appear to have articulated with the intermarginal facets. The median marginals are as tall as broad, and the outer face gently and evenly curved. The sculpture is similar to that on the ultimate superomarginals.

The elongated form of these ossicles suggests that the arm tips of this species were distinctly produced (Wright & Wright 1940). The shape of the ultimate superomarginals is reminiscent of *M. polyplacus* Schulz & Weitschat (1971), but the outer face sculpture of that species differs in having a discrete, raised central area bearing scattered granule pits.

OCCURRENCE. This species of *Metopaster* is known only from the White Hart pit at Wilmington.

Metopaster sp. B

MATERIAL. Two ultimate superomarginals and one median superomarginal collected *in situ* from the lower part of the Wilmington Sands (7·80–9·03 m below datum, Fig. 72; E.54061–3). An ultimate superomarginal and an inferomarginal were collected loose (E.54064).

DESCRIPTION. The ultimate superomarginal ossicles are as broad as long, and flat in proximal profile. The lateral margin is gently curved. The aboral and lateral surfaces of the outer face are discrete. Two inferomarginals were in contact with intermarginal facets on the ultimate superomarginal, of which the proximal one extends over two-thirds of the total length. The outer face bears a distinctive sculpture; on the central part of the aboral surface coarse, hemispherical rugosities are present. The lateral surface bears discontinuous ridges running parallel to the breadth of the ossicle, separated by areas of closely spaced granule pits. The median superomarginal (E.54063) is square in aboral aspect. The aboral surface is flat and on the central part several discrete rounded rugosities are present. The lateral surface is low. The inferomarginal (E.54064) is slightly broader than long; the outer surface is gently curved and carries elongated raised patches of smooth stereom in an irregular, sinuous arrangement. These are separated by areas with fine granule pits.

OCCURRENCE. In England, this species is known only from the White Hart pit at Wilmington. A similar or identical species is known from the Cenomanian of Normandy (G. Breton, personal communication 1980).

Metopaster sp. C

MATERIAL. A single ultimate superomarginal ossicle collected loose in the White Hart pit (E.54065).

DESCRIPTION. The ossicle, which is poorly preserved, is slightly longer than broad. The outer face is strongly curved. The inner border was in contact with aboral ossicles for a third of its length; the aboral facet is set at an angle to the median facet. The outer face is completely obscured by sand pitting.

REMARKS. Significant differences in shape distinguish this ossicle from the other two species of *Metopaster* which occur at Wilmington. It compares most closely with *M. parkinsoni*, a common species in Turonian–Campanian Chalk of western Europe in its proportions and the curvature of the outer face. Better preserved material of the species, showing details of outer face sculpture, is necessary for a certain identification.

Subfamily **Uncertain**

Genus ***CALLIDERMA*** Gray, 1847

TYPE SPECIES. *Calliderma emma* Gray, 1847, by original designation.

Calliderma smithiae (Forbes 1848)

HOLOTYPE. The large specimen displaying the oral surface, figured by Forbes (*in* Dixon 1850: pl. 12, fig. 2). Lower Chalk (Cenomanian), Burham, Kent (BMNH E.25997).

MATERIAL. Three interradial superomarginals, collected *in situ* in the White Hart pit, at 1·42 m and 6·85 m below datum (E.54066–8). Two further superomarginals and an inferomarginal, collected loose from the same locality (E.54069).

DESCRIPTION. The ossicles are poorly preserved. The superomarginals are nearly twice as broad as long. Aboral and lateral surfaces are well demarcated, and set at right angles. At the boundary between the two surfaces, a distinct tumidity is present. The outer face of the superomarginals bears evenly spaced granule pits, which are largest on the tumidity. These ossicles compare closely with the square, tumid interradial superomarginals of individuals of *Calliderma* from the Lower Chalk of south-east England originally described as *Calliderma mosaica* (Forbes 1848), but subsequently synonymized with *C. smithiae* by Spencer (1907). Proximal and distal margins are parallel, reflecting the large disc and broad, gently curved interradii of this morphotype as figured by Forbes (*in* Dixon 1850: pl. 14, fig. 26) and Sladen (1893: pl. 5, fig. 2; pl. 6).

OCCURRENCE. *C. smithiae* is a common species in the basinal marly chalks of Cenomanian age in the Anglo-Paris basin and eastern England. It is rare in the marginal Cenomanian deposits of Devon.

Genus ***OPHRYASTER*** Spencer, 1913

TYPE SPECIES. *Pentagonaster oligoplax* Sladen, 1893, by original destination.

Ophryaster sulcatus (Sladen 1891)
Pl. 42, fig. 1

v 1891 *Tomidaster sulcatus* Sladen: pl. 5, fig. 1.
vp 1907 *Calliderma smithiae* (Forbes); Spencer: 123–124.
[For meaning of convention see Matthews, 1973].

HOLOTYPE. The partially complete disc, displaying the oral surface, figured by Sladen (1891: pl. 5, fig. 1), BMNH E.5063. This specimen is from the Lower Chalk (Cenomanian) of Dover, Kent.

DIAGNOSIS. *Ophryaster* in which the interradial marginals are proportionately high and short. Granule pits cover the outer face. Both supero- and inferomarginals each bear a single slit-like pedicellaria running along the length of the lateral surface. Similar pedicellariae are scattered unevenly on the oral intermediate ossicles.

Plate 42

Ophryaster sulcatus (Sladen)

Fig. 1 E.54070, interradial superomarginal ossicle in aboral view (1a) and profile (1b). Wilmington Sands, 5·14 m below datum, White Hart pit, Wilmington (× 4·6).

Metopaster sp. A

Fig. 2 C. W. Wright colln no. 16571, ultimate superomarginal ossicle in lateral view (2a) and proximal profile (2b). Cenomanian, Wilmington (× 6). (Also figured Wright & Wright 1940: text–fig. 9a–c).

Mastaster villersensis Mercier

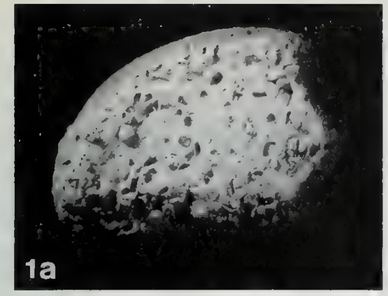
Fig. 3 C. W. Wright colln no. 3535, interradial superomarginal (sml) in distal aspect. Cenomanian, White Hart pit, Wilmington (× 4·3). (Also figured Wright & Wright 1940: pl. 15, fig. 4; Breton 1979: text–fig. 24).

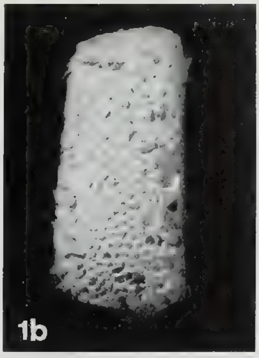
Fig. 4 C. W. Wright colln no. 21949, enlarged interradial superomarginal (sml) in lateral view. Locality as last (× 4·7). (Also figured Breton 1979: text–fig. 24).

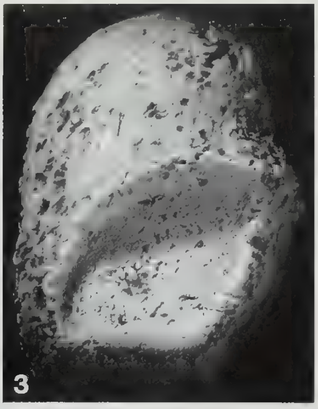
Fig. 5 E.54107, interradial superomarginal (sml) of a juvenile in distal profile (5a) and aboral view (5b). Locality as last (× 4·6).

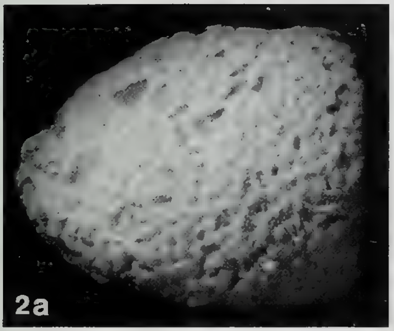
Fig. 6 E.54169, second superomarginal (sm2) in distal profile (6a) and aboral view (6b). Locality as last (× 5·1).

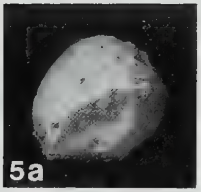
Fig. 7 E.54106, interradial inferomarginal (im1) in oral aspect (7a) and proximal profile (7b). Locality as last (× 4·8).

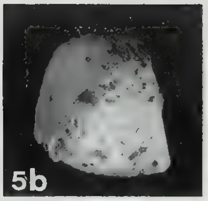

1a

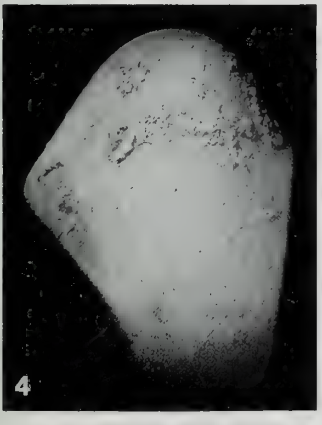

1b

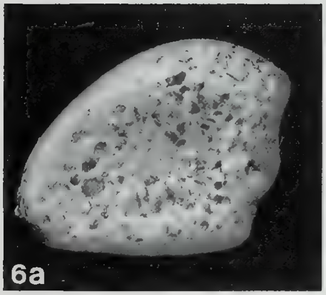

3

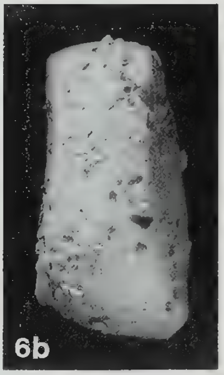

2a

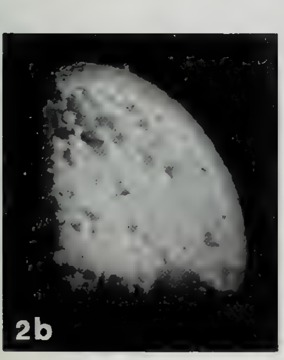

5a

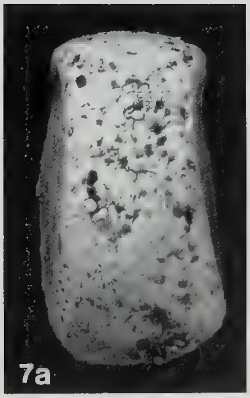

5b

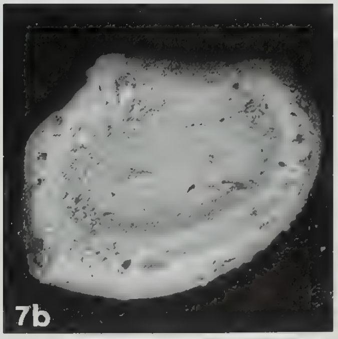

4


6a


6b


2b


7a


7b

MATERIAL. Ten dissociated superomarginal ossicles collected *in situ* from the Wilmington Sands (5·14–9·10 m below datum; E.54070–9) in the White Hart pit. Thirty-five marginal ossicles were collected loose in the same section (E.54080). In the Wrights' collection are two superomarginals (WW 15507–8) from Wilmington.

DESCRIPTION. The interradial superomarginal ossicles are broader than high, and short (Pl. 42, fig. 1). The aboral facet is as tall as the internal face; both are equally concave. The distal and proximal facets are nearly flat with a slightly raised border, and are parallel. In profile (Pl. 42, fig. 1b), the outer face is evenly curved, or poorly demarcated into aboral and lateral surfaces. The outer face (Pl. 42, fig. 1a) bears an even, closely-spaced covering of rather large granule pits. A single slit-like pedicellaria ('elongated type' of Schulz & Weitschat 1971) is present on each ossicle, running obliquely along the length of the outer face just above the intermarginal contact. The inferomarginals are broad with rounded oral surfaces.

AFFINITIES. *O. sulcatus* differs from all other species of the genus by the presence of elongated pedicellariae on the superomarginals and oral intermediate ossicles, and in the absence of a smooth rim on the inner border of the outer face of the superomarginals. From *Comptoniaster comptoni* (Forbes) the species differs in the shape of the marginals and the even distribution of pedicellariae (one on each marginal).

OCCURRENCE. Lower Chalk (Cenomanian) of south-east England. Cenomanian of Devon.

Genus ***COMPTONIASTER*** Breton, 1984

TYPE SPECIES. *Goniaster* (*Stellaster*) *comptoni* Forbes, 1848, by original designation.

Comptoniaster comptoni (Forbes 1848)
Pl. 41, fig. 5

HOLOTYPE. The specimen figured by Forbes (*in* Dixon 1850: pl. 12, fig. 8). Blackdown Greensand (Upper Albian) of Blackdown, Devon. Northampton Museum coll.

MATERIAL. A single distal inferomarginal collected in the Wilmington Sands, at 6·71 m below datum (E.54081). A similar ossicle collected loose (E.54082). Both from the White Hart pit.

DESCRIPTION. The distal inferomarginal figured (E.54081) is as broad as long (Pl. 41, fig. 5b) and proportionately tall. The outer face (Pl. 41, fig. 5a) is moderately curved and is flush with the border; it bears a covering of medium-sized granule pits. Two elongated pedicellariae run parallel on the lateral part of the outer face near the intermarginal contact. The other inferomarginal (E.54082) is similar but only carries a single pedicellaria.

REMARKS. These ossicles are referred to *C. comptoni* on the basis of a close similarity in shape with the distal inferomarginals of a nearly entire specimen of that species (E.34311) from the Blackdown Greensand (Upper Albian) of Blackdown, Devon. In this, the slit-like pedicellariae (which also are found in *Ophryaster*, see above) are not present on all marginals; rarely, two are developed on one ossicle. The angle of the pedicellaria to the ossicle length also varies.

OCCURRENCE. *C. comptoni* is found in the Blackdown Greensand (Upper Albian) of Devon, the Wilmington Sands, and the Cenomanian of Normandy (Breton 1984).

Genus ***CALETASTER*** Breton, 1979

TYPE SPECIES. *C. girardi* Breton, 1979, by original designation.

Caletaster sp.
Pl. 43, fig. 6

MATERIAL. Twelve marginal ossicles were collected *in situ* from 6·18–9·10 m below datum (Fig. 72), in the lower part of the Wilmington Sands (E.54083–94). Seventy-five ossicles were collected loose, also in the White Hart pit (E.54095).

DESCRIPTION. The interradial superomarginals (Pl. 43, fig. 6) are more than twice as broad as long, and show a low, wedge-shaped profile (Pl. 43, fig. 6a). The outer face (Pl. 43, fig. 6b) is nearly as flat or gently and evenly convex, and may be tumid near the inner border. The proximal and distal borders are parallel, or converge slightly towards the lateral margin. The distal superomarginals are as tall as broad and the outer face is evenly and moderately curved. The proximal facet is flat, the distal concave. The outer faces of all marginals are covered with closely spaced, very fine granule pits.

REMARKS. The genus *Caletaster* is characterized by having a large disc and short arms. The interradial marginals are low, broad and proportionately short, and wedge-shaped in profile. Granule pits on the outer face are very fine. The Wilmington ossicles agree with the type species (*C. girardi*) in all these regards, but are consistently smaller and proportionately broader.

A further undescribed species of the genus occurs in the Lower Chalk (Cenomanian) of south-east England (E.28303, E.377).

Genus ***CRATERASTER*** Spencer, 1913

TYPE SPECIES. *Asterias quinqueloba* Goldfuss, 1831, by original designation.

Crateraster quinqueloba (Goldfuss 1831)

MATERIAL. A single superomarginal, collected loose in the White Hart pit (E.54111).

DESCRIPTION. The proximal superomarginal is as broad as high. The distal facet is slightly broader than the proximal one, such that the inner border is angled to the lateral border. Lateral and aboral surfaces are well demarcated and set at right angles. The outer surface bears large, evenly spaced granule pits the interstices of which are raised to create low, poorly defined rugosities.

Comparison with well-preserved individuals of *C. quinqueloba* from the Chalk of southern England allows the ossicle to be placed as a SM2, on account of its shape.

OCCURRENCE. *C. quinqueloba* is a common and widespread species in the Chalk (Cenomanian to Campanian) of western Europe.

Genus ***MASTASTER*** Mercier, 1935

TYPE SPECIES. *Mastaster villersensis* Mercier, 1935, by monotypy.

Mastaster villersensis Mercier 1935

Pl. 42, figs 3–7; Pl. 43, fig. 3

HOLOTYPE. This was the well-preserved individual from the Cenomanian of Villers-Sur-Mer in Calvados, Normandy (Mercier 1935: pl. 3, fig. 1); it was in the collection of the University of Caen, destroyed during the Second World War. No neotype has been designated.

MATERIAL. Ten marginal ossicles were collected *in situ* from the Wilmington Sands (4·56–9·40 m below datum; E.54096–105) in the White Hart pit. Loose at the same locality, 220 marginal ossicles were collected (E.54106–8). In the Wrights' collection there are ten interradial superomarginals (SM1) from Wilmington (WW 2009, 2472, 2120, 2010, 21949, 20754, 14128, 3535, 18996).

DESCRIPTION. The pair of aborally swollen superomarginals which occupy each interradius are the largest and most conspicuous ossicles in the species and are disproportionately represented in the collections.

The first-formed superomarginals (SM1) are approximately as broad as long (Pl. 42, figs 3, 4) and are proportionately tall. The distal facet is inclined to the flat, vertically positioned proximal facet at an angle between 40 and 50° (Pl. 42, fig. 4). The distal facet is two-thirds of the height of the proximal and is concave. The lateral surface is vertical and tumid. The aboral part of the ossicle is produced into a vertically positioned protuberance, which may be bulbous (Pl. 42, fig. 3), parallel-sided with a rounded top (Pl. 42, fig. 4) or conical (Breton 1979: text-fig. 24). When well preserved, the outer face is covered by very fine, closely spaced granule pits.

The second superomarginals (SM2) (Pl. 42, fig. 6) are as tall as broad and half as long. The proximal facet is inclined distally to the horizontal plane at an angle of 40–50°, in order to accommodate the slanted facet on the adjacent SM1. The distal facet is concave and nearly vertical in orientation. The outer face is slightly swollen aborally. A short lateral surface is present (Pl. 42, fig. 6a).

The distal superomarginals (Pl. 43, fig. 3) are as broad as tall and are square in aboral aspect. The outer face is gently and evenly curved (Pl. 43, fig. 3a). Both proximal and distal facets are concave, the distal more strongly so (Pl. 43, fig. 3b). One ossicle clearly shows an outer face sculpture of very fine, closely-spaced granule pits; others are apparently smooth.

The proximal inferomarginals (IM1) are as tall as broad and half as long (Pl. 42, fig. 7). The outer face is demarcated into a strongly curved oral surface, and a short, curved lateral surface. The proximal border is straight; the proximal facet is vertical and nearly flat. The distal facet is concave, and bears a stout articulation ridge along the oral margin (Pl. 42, fig. 7b). The distal inferomarginals are as broad as high, with gently and evenly curved outer faces.

On many of the Wilmington ossicles of *Mastaster* the outer face sculpture is obscured by sand pitting or decorticated. The majority, however, do appear to be devoid of granule pits. These are only commonly seen on the large interradial superomarginals (e.g. Pl. 42, fig. 4). However, a small number of ossicles display a highly distinctive and different surface sculpture. This consists of slightly raised, flat-topped patches of smooth stereom, in irregularly rounded areas or in a rectilinear configuration. The intervening surface bears fine granule pits. This is seen most commonly on distal inferomarginals, but is rarely found on superomarginals from different positions in the radius. This sculpture is also seen on marginals from the Beer Head Limestone of the Devon coast (e.g. BGS no. Yd 4388).

ONTOGENY. A large number of SM1 are present in the collection; these show a considerable range in size. The smallest ossicle (L : 3·7, B : 3·9, H : 3·3 mm) has a narrower distal facet than proximal, as in the adult (Pl. 42, fig. 5). The ossicle is evenly tumid on the lateral and aboral surfaces (Pl. 42, fig. 5a). The SM1 grows in this proportion until about 5 mm in length, when increased height is achieved by development of the aboral protuberance. The largest SM1 known from Wilmington (L : 10·6, B : 3·9, H : 14·0 mm) illustrates this proportional change.

OCCURRENCE. *M. villersensis* is found in marginal sands and sandy limestones of Cenomanian age in south-west England and north-west France. In England, it is found in the Rye Hill Sands of Warminster, Wilts. (BMNH and BGS collections), the Beer Head Limestone of the Devon coast, at Wilmington, and in Middle Cenomanian 'Basement beds' at Punfield, Dorset (Wrights' colln) and Snowden Hill, Chard (Milton-Worsell colln).

Mastaster sp.

Pl. 43, fig. 4

MATERIAL. Sixteen superomarginals collected loose in the White Hart pit at Wilmington (E.54109–10).

DESCRIPTION. The interradial superomarginals, the only ossicle type certainly known, are approximately as broad as high, and proportionately short (Pl. 43, fig. 4). The proximal and distal borders are parallel; the latter is slightly less broad. The upper part of the aboral surface is produced into a small, rounded tumidity. The lateral surface is low and vertical. The proximal and distal borders of the outer face are slightly depressed, and the central region is raised. The outer face is smooth. An immature SM1 of the same species is present amongst the material. This has dimensions L : 3·9, B : 4·7, H : 3·5 mm. It may be distinguished from the equivalent ossicles of juvenile *M. villersensis* by the restriction of the swelling to the aboral part of the ossicle.

REMARKS. Breton (1979) described a subspecies *M. villersensis wrighti* on the basis of a well-preserved individual from St Jouin on the Normandy coast. This he distinguished from the nominal species on the virtual absence of granule pits from the marginal ossicles, and the weakly developed aboral protuberance on the interradial superomarginals (SM1). He stressed that the distinction between the subspecies was entirely morphological. Through the courtesy of M. Breton, I have received a plaster cast of the holotype of *M. villersensis wrighti* (MHNH 2247A). The ossicles from Wilmington compare with this specimen in lacking granule pits entirely. However, the interradial superomarginals (SM1) differ significantly in shape between the two. The Wilmington ossicles are parallel-sided, in contrast to those of *M. villersensis wrighti*, and possess a discrete aboral tumidity which is lacking on that subspecies.

OCCURRENCE. Cenomanian of Wilmington.

Goniasteridae species A

Pl. 43, figs 1, 2

MATERIAL. Two superomarginal ossicles were collected *in situ*, one in the Grizzle (2·66 m below datum; E.54112) and one in the upper part of the Wilmington Sands (4·22 m below datum; E.54113) in the White Hart pit (see Fig. 72). Thirty infero- and superomarginals were collected loose (E.54114). Two superomarginals from Wilmington are present in the Wrights' collection (WW 12183).

DESCRIPTION. The superomarginals are approximately as broad as high and proportionately short (Pl. 43, figs 1, 2). The aboral and lateral surfaces are well demarcated in most ossicles and set nearly at right angles. At the boundary between the two surfaces a tumidity is present on many of the superomarginals (Pl. 43, figs 1c, 2c). A few superomarginals are evenly and strongly rounded in profile, such that the outer face describes two-thirds of a circle. The outer surface bears a covering of irregularly-sized polygonal granule pits which are more deeply impressed on the tumidity (Pl. 43, figs 1b, 2b). The proximal and distal borders are parallel, the distal border being slightly concave. The distal facet is concave; the aboral facet is concave, and equal in height to the internal face.

The distal facet of each superomarginal (Pl. 43, figs 1c, 2c) bears a short, rounded protuberance near the inner border, on the lateral side of which is a shallow groove. This corresponds with a socket and low ridge on the proximal facet of each face (Pl. 43, figs 1a, 2a).

The inferomarginals have proportionately long, evenly curved oral surfaces and low lateral surfaces. A socket and ridge articulation is present on the proximal and distal facets. The outer face is covered with even-sized granule pits.

REMARKS. The rectangular aboral profile of the superomarginals suggests that the asteroid had a broad disc with evenly curved interradii. The superomarginals did not meet over much of the arm length, as indicated by the absence of facets articulating adjacent rows of ossicles. The implied shape of the entire asteroid, together with the shape and outer face sculpture of the marginals, are consistent with a genus such as *Calliderma* or *Tylasteria*. However, the ossicles are distinguished from any fossil or Recent species of goniasterid by the presence of a ball and socket articulation between adjacent marginals. This probably served to strengthen the marginal frame by preventing lateral shearing between marginal ossicles.

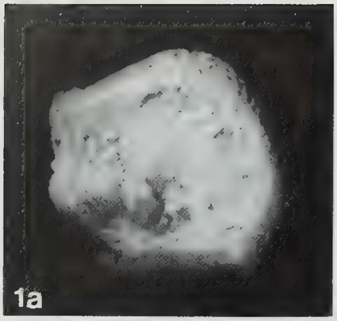
OCCURRENCE. Cenomanian of Wilmington, Devon.

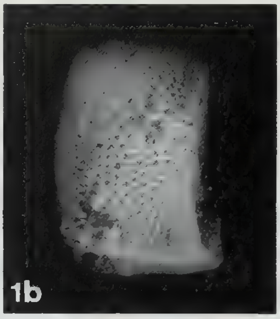
Goniasteridae species B

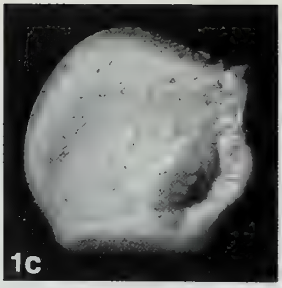
Pl. 43, fig. 5

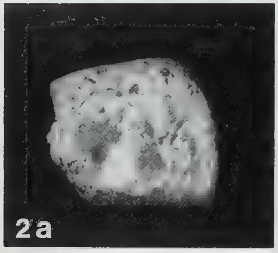
MATERIAL. Nine marginal ossicles collected *in situ* in the White Hart pit from the Wilmington Sands (4·07–9·58 m below datum; E.54116–124). Fifty marginals were collected loose (E.54115, 54125) at the same locality.

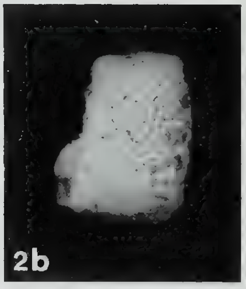
DESCRIPTION. The interradial superomarginals are twice as broad as long and wedge towards the lateral border. They are low in profile; the aboral surface is weakly curved. The aboral facet

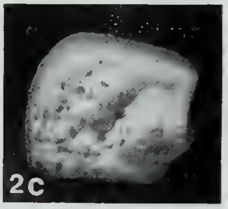

1a

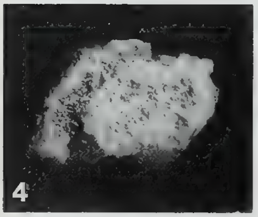

1b

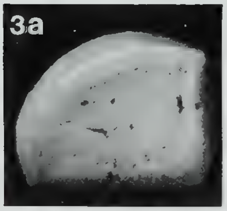

1c

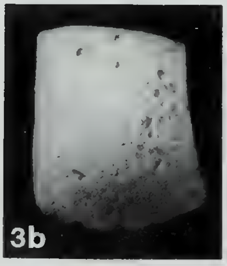

2a

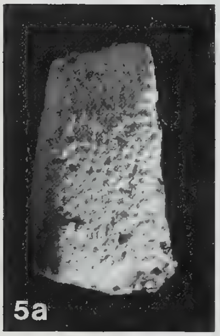

2b

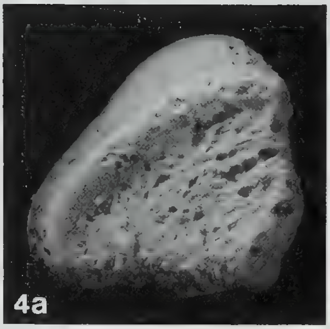

2c

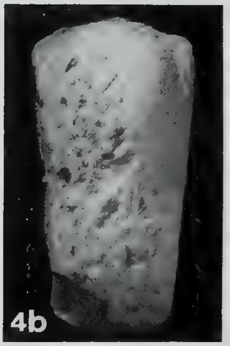

4

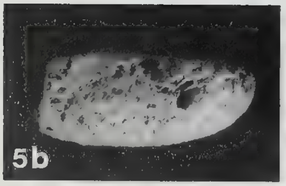

3a

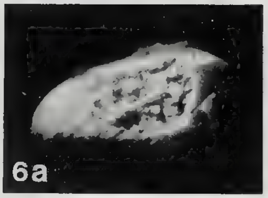

3b

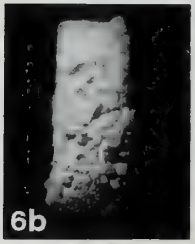

5a


4a


4b


5b


6a


6b

is slanted inwards, hidden under the inner border of the superomarginals. The internal face is at a low angle to the intermarginal facet. The more distal superomarginals are rectangular in aboral aspect. The proximal facet is strongly concave; the distal is convex. The distal superomarginals are nearly square, and met over the mid-radial line for at least the distal part of the arm, as indicated by the replacement of aboral facets by those uniting adjacent rows of superomarginals. The superomarginals bear, on the outer face, a covering of unevenly sized small rugosities cojoined by short ridges. Granule pits are created by the interstices of the rugosities and ridges.

The inferomarginals (Pl. 43, fig. 5) are similar to equivalent superomarginals in shape. They may most readily be distinguished by the nearly vertical orientation of the oral facet (Pl. 43, fig. 5b); the rugosities are replaced by an even covering of rounded granule pits.

Remarks. The presence of wedge-shaped interradial marginal ossicles in asteroids is indicative of short, acutely angled interbrachial arcs (Blake 1973). In addition, the superomarginals of this species met over at least part of the arm. The species cannot be accommodated in any known goniasterid genus.

Occurrence. Goniasteridae species B is known from the Wilmington Sands of the Wilmington outlier, and from the lower part of the Beer Head Limestone (Cenomanian) on the Devon Coast.

Order **PAXILLOSIDA** Perrier, 1884

Family **ASTROPECTINIDAE** Gray, 1840

Diagnosis. Body flat, conspicuous rows of opposing supero- and inferomarginals present. Pairs of marginals are separated by aboral–oral grooves which carry intermarginal fascioles. Dorsal surface consists of paxillae set in a flexible integument.

Genus *COULONIA* de Loriol, 1874

Coulonia sp.

Pl. 43, fig. 7

Material. Four marginal ossicles collected *in situ* from the Wilmington Sands, 7·19–11·50 m below datum. These include two superomarginals (E.54170–1) and two inferomarginals (E.54172–3). Five superomarginals were found loose in the White Hart pit (E.54168).

Plate 43

Goniasteridae species A

Fig. 1 C. W. Wright colln no. 12183, superomarginal in distal profile (1a), aboral view (1b) and distal profile (1c). Cenomanian, Wilmington (× 5·1).

Fig. 2 E.54112, superomarginal in proximal profile (2a), aboral view (2b) and distal profile (2c). Grizzle, 2·66 m below datum level, White Hart pit, Wilmington (× 5).

Mastaster villersensis Mercier

Fig. 3 E.54096, distal superomarginal in proximal profile (3a) and aboral view (3b). Grizzle, 2·54 m below datum level, White Hart pit, Wilmington (× 5·1).

Mastaster sp.

Fig. 4 E.54109, interradial superomarginal (sm1) in profile (4a) and aboral (4b) view. Collected loose, White Hart pit, Wilmington (× 4·8).

Goniasteridae species B

Fig. 5 E. 54115, inferomarginal in oral view (5a) and distal profile (5b). As last (× 5).

Caletaster sp.

Fig. 6 E.54083, superomarginal ossicle in profile (6a) and aboral view (6b). Wilmington Sands, 6·58 m below datum level, White Hart pit, Wilmington (× 4·9).

Coulonia sp.

Fig. 7 E.54168, superomarginal ossicle in profile. Bed A1, 11·50 m below datum level, White Hart pit, Wilmington (× 4·4).

DESCRIPTION. The interradial superomarginals are short and broad and in aboral aspect narrow towards the lateral border (Pl. 43, fig. 7). In profile, they are triangular. The outer face is gently curved and bears large, rounded spine pits. The proximal and distal facets are separated into raised articulation ridges and flat fasciolar surfaces (Pl. 43, fig. 7), as in all astropectinids (Blake 1973). The articulation ridge extends across two-thirds of the breadth of the ossicle. Near the inner margin of the ossicle, the border of the articulation ridge runs parallel to the outer face, but deflects vertically near the lateral border. More distal superomarginals are nearly rectangular in profile and have indiscrete lateral surfaces. The fasciolar surfaces are narrow and the articulation ridge parallels the outer face across the breadth of the plate.

The inferomarginals are tall and bear large, horseshoe-shaped spine bases on the outer surface.

REMARKS. Astropectinid marginal ossicles from Albian and Cenomanian deposits all over southern England have been referred to *Lophidiaster ornatus* Spencer, 1913 (Wright & Wright 1940). The type specimen of *L. ornatus* comes from the Lower Albian Folkestone Sands of Folkestone (Casey 1961) and is preserved in the Sedgwick Museum, Cambridge (B 17718); it retains many ossicles in their natural positions. However, all ossicles are deeply weathered and sand-pitted and no details are visible; the specimen must be considered Astropectinidae *incertae sedis*.

The Wilmington ossicles compare closely with dissociated astropectinid ossicles which occur commonly in the Chert Beds of the Upper Greensand (Upper Albian) on the Devon and west Dorset coast (Gale colln, BGS Yd 4371–4; Wrights' colln WW 20982–3, 19298). These are characterized by broad lateral fasciolar surfaces on the interradial marginals, and the vertically deflected lateral margin of the articulation ridge. The outer surface of the superomarginals is evenly rounded and bears a few large spine pits. These ossicles are referred to the genus *Coulonia* on comparison with material figured by Hess (1955: figs 16–22) under the name of *Cuneaster hauteriviensis*. Hess (1970) subsequently considered this name to be a junior synonym of *Coulonia neocomiensis* de Loriol, 1874.

It is hoped to revise the Cretaceous Astropectinidae of north-west Europe in the near future.

Crinoids

by C. R. C. Paul and S. K. Donovan

Introduction

Crinoids form a relatively minor element of the echninoderm fauna at Wilmington, although isolated columnals and fragments of the stems of isocrinids are common fossils. Both stalked (isocrinid) and free-living (comatulid) crinoids occur at Wilmington, but the faunal diversity was low. Although Cretaceous crinoids have received relatively little study, Rasmussen (1961) produced a comprehensive monograph of the entire Cretaceous crinoid fauna. It was surprising, therefore, to discover that the commonest crinoid present at Wilmington represents a new species of isocrinid. Carpenter (1880*a*, *b*) described several British Cretaceous comatulid crinoids, including two now found at Wilmington. Gislén (1924, 1925) revised the taxonomy of comatulids in general, including several British species, but the only published reference to crinoids from Wilmington is in Rasmussen (1961: 296), where a single specimen of *Glenotremites rotundus* (Carpenter) is recorded. Rasmussen (1961; and *in* Rasmussen & Sieverts-Doreck 1978) are the standard references for Cretaceous crinoids and the articulates, respectively.

Terminology follows Rasmussen (1961), Moore, Jeffords & Miller (1968), Breimer (1978), Ubaghs (1978) and Donovan (1984). Principal features and measurements are illustrated in Figs 74 and 75. All figures in the plates are scanning electron micrographs of specimens coated with gold/palladium. Unless otherwise stated, all the figured specimens were collected loose at Wilmington.

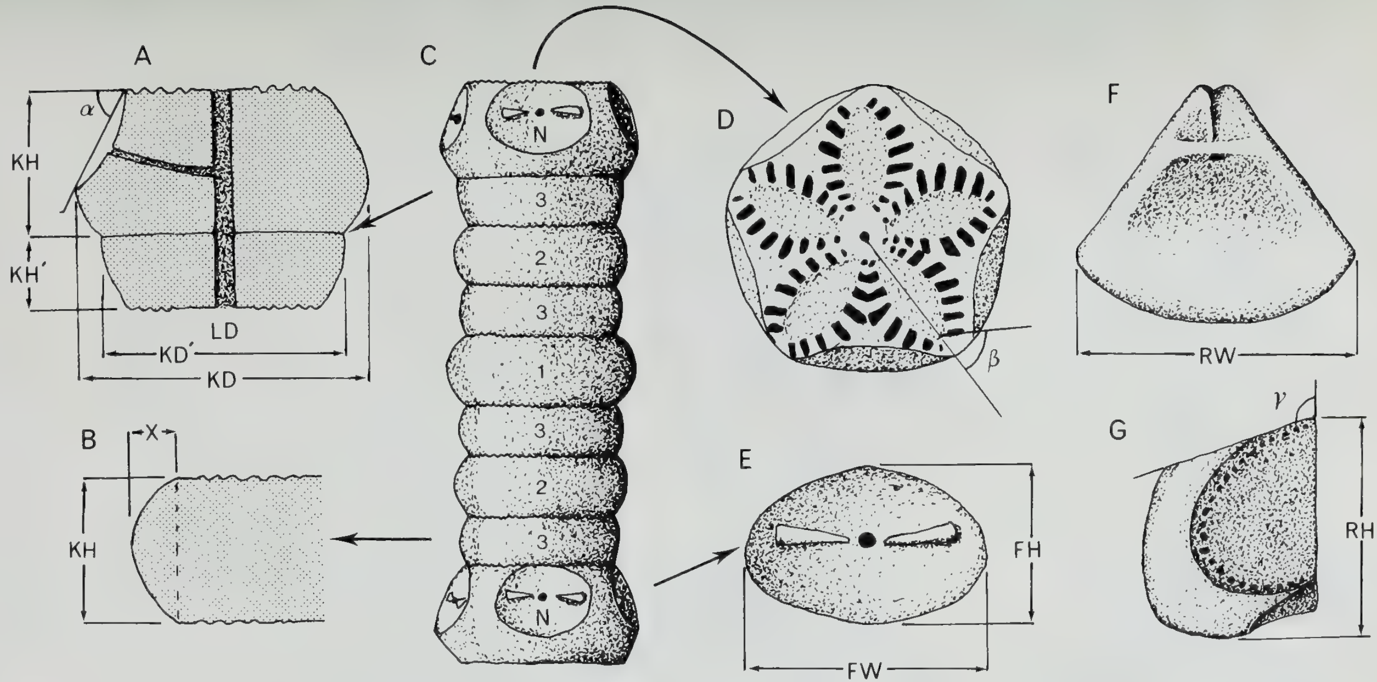


Fig. 74 Diagrams to illustrate the general morphology and principal measurements of isocrinid stems (A–E) and radials (F–G). A, cross-section through a nodal (above) and internodal. KD diameter of nodal columnal, KD′ diameter of internodal, KH height of nodal, KH′ height of internodal, LD diameter of lumen of the stem. α angle between the horizontal and the plane of the cirral facet. Nodal indices for diameter and height, KD′ : KD and KH′ : KH, respectively. B, cross-section through the edge of a columnal to illustrate measurement of convexity, the latus index, which is given by 100X/KD. C, stylized noditaxis of a column showing two nodals and three orders of internodals. The complete noditaxis in this example is N3231323 in the Webster (1974) notation. D, articulum of an internodal columnal showing the petalloid arrangement of crenellae. Petals are open and β is the angle between the most peripheral crenellae and a radius. E, detail of a cirral facet on a nodal showing the two synarthrial ridges on either side of the cirral lumen. FH facet height, FW facet width. Facet concavity may be expressed in the same way as the latus index (100x/FW). F, ventral view of the brachial facet on an isolated radial plate. Note the synarthrial ridge (horizontal), food groove (above) and dorsal ligament pit (below). RW radial width. G, lateral view of an isolated radial plate showing external surface (left), radial : radial facet with weak peripheral crenellae (right) and small radial : basal facet (below right). RH radial height, γ the angle between the vertical axis and the plane of the brachial facet. Diagrams not to scale.

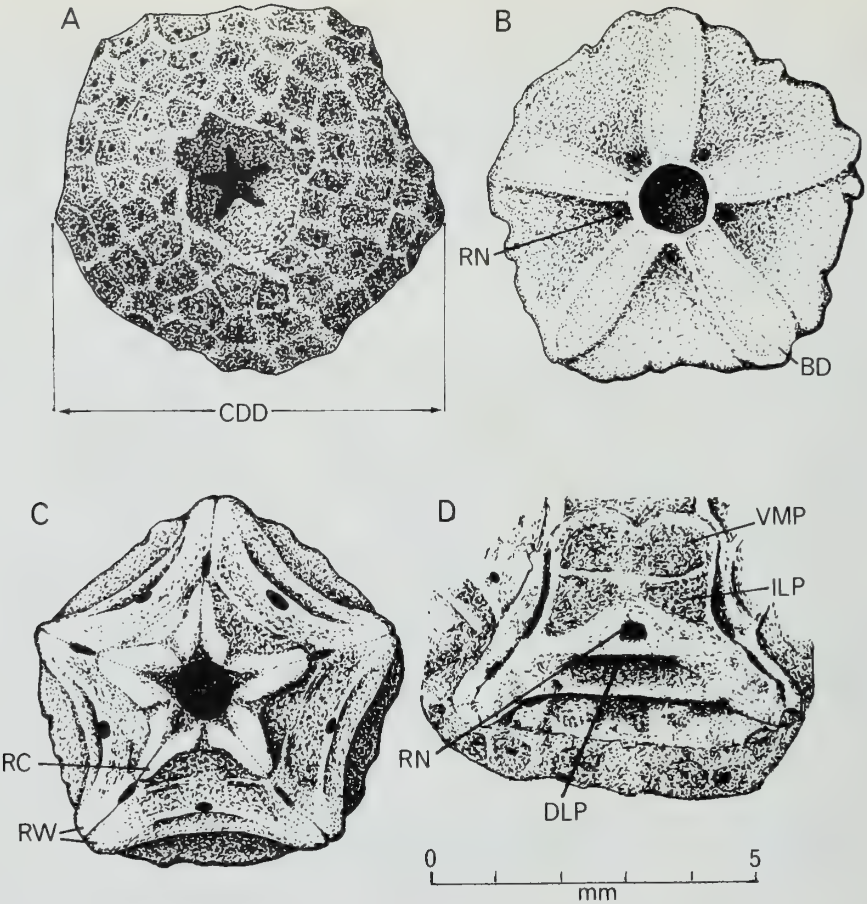


Fig. 75 Camera lucida drawings to illustrate the basic morphology of comatulid crinoids. A, dorsal view of centrodorsal plate of *Glenotremites rotundus* (Carpenter) to show the cirral facets and prominent dorsal star. E.51657, Albian, Blackdown Greensand, Blackdown, Devon. (CDD, centrodorsal diameter.) B, ventral view of same centrodorsal to show the central cavity surrounded by five shallow depressions for the basal plates (BD) and five small radial nerve canals (RN). C, ventral view of complete cup of *Glenotremites* cf. *aequimarginatus* (Carpenter) to show central body cavity, radial crests (RC) and radial wings (RW). E.69803, collected loose at Wilmington. D, oblique lateral view of one brachial facet in *Glenotremites* cf. *aequimarginatus* (Carpenter) to show muscle and ligament pits. DLP, dorsal ligament pit; ILP, interarticular ligament pit; RN, radial nerve canal; VMP, ventral muscle pit. E.69802, collected loose at Wilmington.

Palaeoecology and preservation

All specimens from Wilmington have suffered pressure solution and are more or less badly pitted by sand grains so that surface features are often obscured. Nevertheless, some undamaged areas occur on most specimens and it is usually easy to assign them to one of the species recognized.

No complete crinoids are known at Wilmington. Isocrinids occur as isolated columnals, radials or short pluricolumnals which never include more than one noditaxis and only very rarely have any cirrals attached. Comatulids are known from isolated centrodorsals or complete cups, which never have cirrals or brachials attached. Most comatulid cups show evidence of abrasion—some of which may be recent, however. This, together with the general coarseness of the sediment, suggests a relatively high energy environment. Many stems, whether single plates or groups of plates, show evidence of wear and boring by various organisms. Some crinoids may have been exhumed more than once. Epifauna of bryozoans, sponges and worm tubes is not at all uncommon; most must have attached after death of the crinoid. In cases where epifauna coats articulation surfaces and cirral facets this can be demonstrated unequivocally. It seems obvious that most specimens lay on the sea floor for some time before final burial. About 40% of the isocrinid specimens consist of pluricolumnals, so that total disarticulation did not always occur. This proportion does not change significantly throughout the Cenomanian section. Crinoid remains are commonest in the sands which probably accumulated relatively rapidly. This concentration is unlikely to be an artefact of variations in the rate of sediment accumulation: certainly the remains have not been concentrated in a lag deposit. Furthermore, the concentration is unlikely to reflect uneven collecting since the greatest concentration of crinoid remains occurs where echinoids are relatively rare. The only radials and the only comatulid known *in situ*, as well as the last known examples of *?Isocrinus cenomanensis* (d'Orbigny), occur at this level. Preservation of loose specimens of *Glenotremites* also suggests that many of them came from uncemented sands (i.e. not the Grizzle or Wilmington limestone). All of this suggests that the concentration of specimens is real and that both isocrinids and comatulids were adapted to life in moderate currents on an unconsolidated substrate.

The isocrinids seem to have had fairly robust stems. *?I. cenomanensis* probably had a more flexible stem than *?I. undulatus* sp. nov. In both species the variations in the dimensions of the nodals and internodals may well result from rapid growth. The only known radial plates, which are believed to belong to *?I. undulatus*, have almost horizontal brachial facets (Pl. 46, fig. 1), which suggests that the arms of this species were not extensively branched and could fold up over the cup to form a very streamlined crown which would offer less resistance to currents. Similarly, the upwardly-directed cirri of *?I. undulatus* would also have reduced resistance to currents.

Pathological anomalies

Deformed or injured specimens of crinoids are rare at Wilmington and so far there is no evidence of parasitism. However, a few anomalous specimens have been found. Specimen E.69650 (Pl. 44, fig. 4) is a pluricolumnal of *?I. cenomanensis* with six-fold symmetry. It originated from the proximal stem as it bears six canaliculi on the cryptosymplectial articulation of the nodal, which nevertheless bears only five cirral facets. Three further anomalous specimens of *?I. undulatus* have also been found; in this species anomalous pluricolumnals with fewer than five cirri. E.69684 is a pluricolumnal composed of three internodals above a nodal which has only one cirral facet. E.69685 is a pluricolumnal consisting of the infranodal and a nodal with only three adjacent cirral facets. Both the nodal and infranodal have grooves bounding the abnormal part and may have regrown after injury. Finally, E.69686 is a pluricolumnal with the infranodal and a nodal which has four cirral facets, but appears to be uninjured.

Stratigraphical distribution

The stratigraphical distribution of crinoids at Wilmington is summarized in Fig. 76. As mentioned above, the variations in abundance are probably real. *?I. cenomanensis* is relatively rare and only occurs in the lower part of the section, where it extends from the so-called Upper Greensand into the Wilmington Sands. *?I. undulatus* first appears in the basement bed and reaches up to the Wilmington Limestone. Radials have been found *in situ* only where *?I. undulatus* is most abundant. This and the similarity in surface ornament (both are virtually smooth) suggest that the radials belong to *?I. undulatus*. Only a single specimen of *Glenotremites* cf. *aequimarginatus* (Carpenter) has been found *in situ*, also at this level, so it is impossible to comment on its distribution, although loose specimens have the same preservation and probably came from the Wilmington Sands. E.69301, another example of *G.* cf. *aequimarginatus*, was collected *in situ* 'in sands about 25′ below the Grizzle' according to the label. This would put it at approximately 11 m below datum in our section and well into the 'Upper Greensand'.

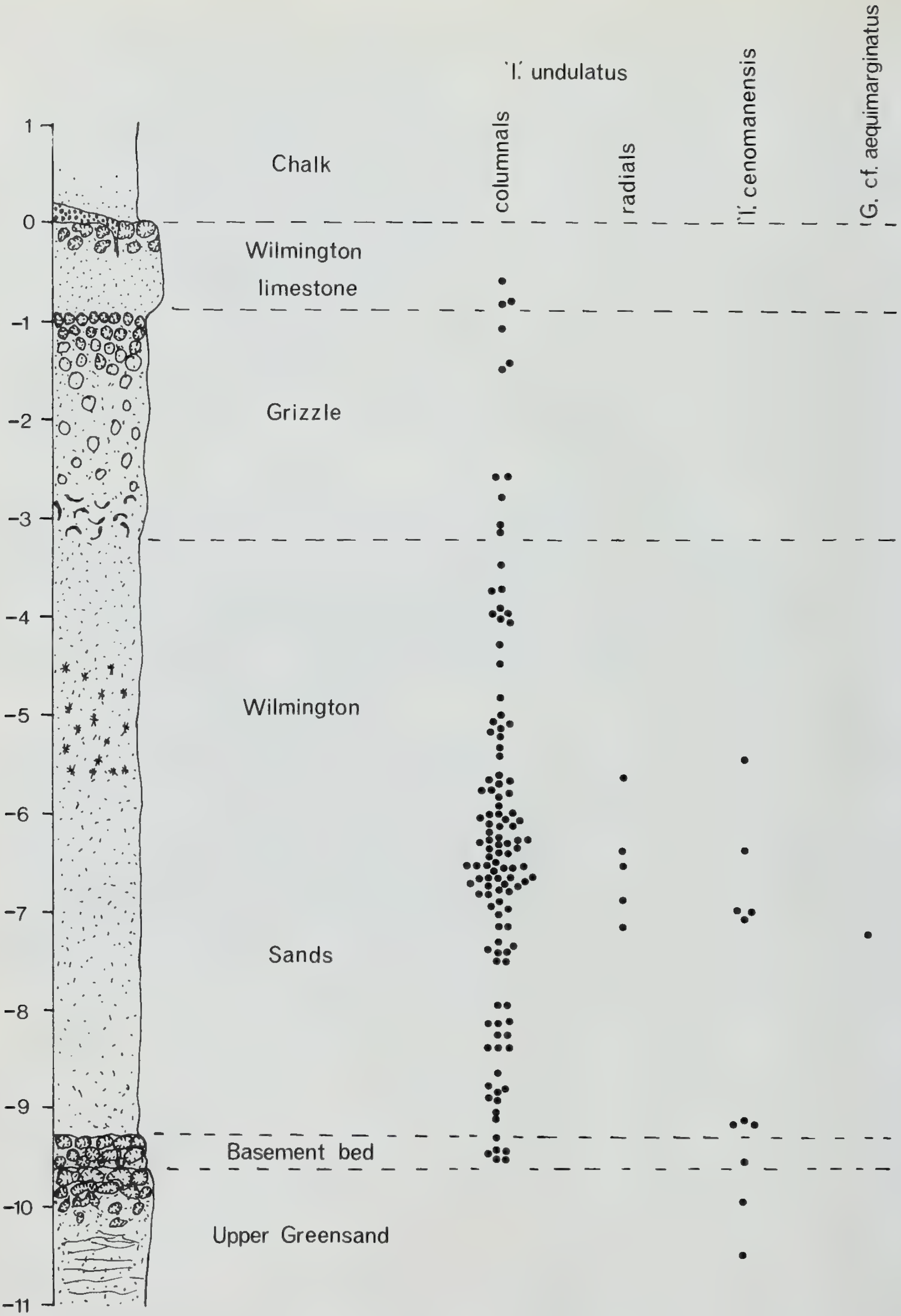


Fig. 76 Stratigraphical distribution of crinoids at the White Hart pit, Wilmington, Devon. Each dot represents a single specimen.

However, the description 'in sands' implies a higher level within the Wilmington Sands and we believe that no comatulid has yet been recorded from the 'Upper Greensand'.

Evolutionary changes

Too few specimens have been collected *in situ* to be sure of any evolutionary changes, but there are some indications of variation which are worth mentioning. Typical *?I. cenomanensis* has a low KH : KD ratio and a high latus index owing to the sharply angled keel around the latus. Examples with relatively thicker columnals and weaker keels (Pl. 44, figs 6, 7), resembling specimens from the Upper Cenomanian of France which Valette (1917) described as *?I. neuvillensis*, occur at Wilmington. Only one is known *in situ* at the top of the range for this species. In this form the diameters of nodal and internodals do not differ as much as in typical *?I. cenomanensis* so that this feature may also have declined up through the section, but again too little information is available. *?I. cenomanensis* probably evolved from the Aptian–Albian species *?I. arduennensis* Valette.

Typical *?I. undulatus* have high latus and nodal indexes, but again, near the top of the range of this species, forms with planar latera and no variation in columnal diameter along the stem occur (Pl. 47, fig. 4). They may represent specimens evolving towards the Turonian species *?I. granosus* Valette, but are too rare for us to be certain of this. *?I. undulatus* probably evolved from the Albian species *?I. cretaceus* (Leymerie), which is not a species of *Nielsenicrinus* as interpreted by Rasmussen (1961), nor does it range above the Albian as far as we are aware. The fairly complete specimen from the Cenomanian of Folkestone illustrated by Rasmussen (1961: pl. 12, figs 5a–b) and on which he based the assignment of *I. cretaceus* to *Nielsenicrinus*, is neither a true *?I. cretaceus* nor a *?I. undulatus*, but has some resemblance to Valette's species *?I. neuvillensis*.

Systematic descriptions

The species of crinoids described in this paper are classified as follows.

- Class Crinoidea Miller 213
  - Subclass Articulata Zittel 213
    - Order Isocrinida Sieverts-Doreck 213
      - Genus *?Isocrinus* Agassiz 214
        - *?Isocrinus cenomanensis* (d'Orbigny) 214
        - *?Isocrinus undulatus* sp. nov. 216
        - *?Isocrinus* cf. *granosus* Valette 222
    - Order Comatulida Clark 222
      - Superfamily Notocrinacea Mortensen 224
        - Family Notocrinidae Mortensen 224
          - Genus *Glenotremites* Goldfuss 224
            - *Glenotremites rotundus* (Carpenter) 227
            - *Glenotremites* cf. *aequimarginatus* (Carpenter) 230
            - *Glenotremites* cf. *paradoxus* Goldfuss 231
            - *Glenotremites* cf. *discoidalis* Gislén 231
            - *Glenotremites* sp. 233

Class **CRINOIDEA** Miller, 1821

Subclass **ARTICULATA** Zittel, 1879

Order **ISOCRINIDA** Sieverts-Doreck, 1952

DIAGNOSIS. Articulate crinoids with a functional stem in adults, with repeated nodals that bear (usually) five lateral cirri. Cup dicyclic or cryptodicyclic, radials with large muscular brachial articulation facets. Arms always branch at least once to give a minimum of ten arms, first division on IBr_2 (except in *Metacrinus* where 4–7 IBrBr occur).

REMARKS. Currently the order is divided into four families (Rasmussen, *in* Rasmussen & Sieverts-Doreck 1978). The Triassic Holocrinidae (two genera) have obvious infrabasals, all other families do not. Holocrinids also lack petaloid articula on columnals, as does the Recent genus *Proisocrinus* which is placed in a separate family of its own. The Jurassic genera *Pentacrinites* and *Seirocrinus* are placed in the family Pentacrinitidae. They are characterized by basals which extend down over the uppermost part of the proximal stem and by radials which lack distinct muscle pits on their brachial articulations. All other genera (at least 15) are placed in the Isocrinidae. Within this family genera are distinguished primarily on details of the branching of, and the distribution of non-muscular articulations in, the arms. Although two or three genera were originally defined on stems alone, most fossil forms cannot be assigned to a genus with certainty and are referred to *?Isocrinus*. This is the case with the Wilmington material.

Genus *?ISOCRINUS* Agassiz, 1836

?Isocrinus cenomanensis (d'Orbigny 1850)
Pl. 44; Figs 77C, D

1850 *Pentacrinus cenomanensis* d'Orbigny: 180
?1917 *Isocrinus neuvillensis* Valette: 138, fig. 18, 1.
1961 *?Isocrinus cenomanensis* (d'Orbigny); Rasmussen: 118; pl. 17, figs 5–8 (?fig. 4 = holotype of *I. neuvillensis* Valette).

DIAGNOSIS. A species of *?Isocrinus* with thin columnals having angular latera ornamented with irregular ridges and a central keel; articula with open petals of 12–14 crenellae, the last at a high angle to the radius. Nodals with strongly concave, oval cirral facets which occupy 80–100% of the nodal height and lie almost parallel to the axis. Nodals slightly larger than internodals. Noditaxis of up to 11 columnals.

TYPE SPECIMEN. D'Orbigny did not select a holotype, nor did he figure a specimen. Rasmussen (1961: pl. 17, figs 5–6) illustrated two examples from d'Orbigny's collection, but neither came from the cited type locality. It is doubtful whether a suitable type specimen now exists in d'Orbigny's collection. No neotype has been designated.

MATERIAL. About 100 columnals and pluricolumnals from Wilmington, of which 13 were collected *in situ*.

HORIZONS. At Wilmington *?I. cenomanensis* ranges from 1044 cm up to 638 cm below datum and thus extends from the Upper Greensand into the middle of the Wilmington Sands. On the coast, *?I. cenomanensis* is even rarer and is known from 308 cm to 422 cm above the Small Cove Hardground, i.e. it is apparently confined to the Hooken Member of the Beer Head Limestone Formation.

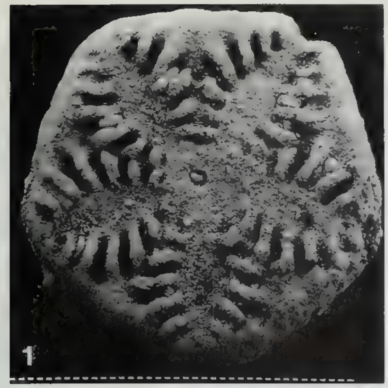
DESCRIPTION. *?I. cenomanensis* is only known from stem fragments. Columnals are pentagonal in cross section (Pl. 44, fig. 1), are relatively thin (Pl. 44, fig. 4), and have ornamented, angular latera and open petals (Pl. 44, fig. 2).

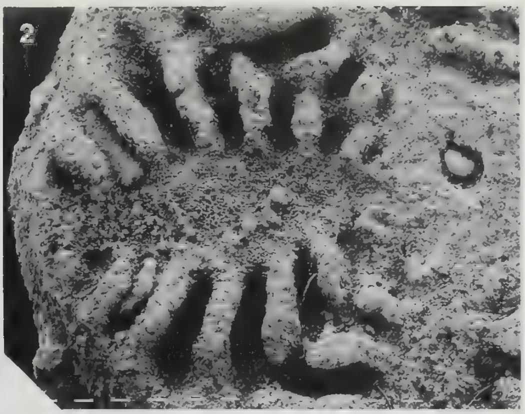
Plate 44
?Isocrinus cenomanensis (d'Orbigny)

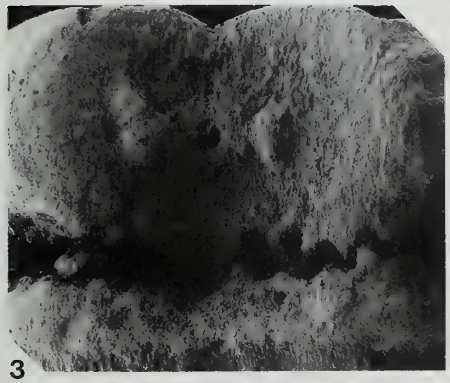
Figs 1, 2 E.69649, isolated internodal: 1, articulum (× 10). 2, detail of one petal (× 25). Note the open petal with peripheral crenellae at a high angle to the radius.

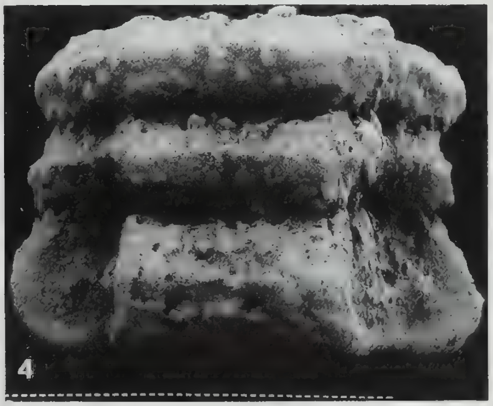
Figs 3, 4 E.69650, abnormal pluricolumnal (with six-fold symmetry) which consists of a nodal and two internodals: 3, detail of the cirral facet (× 17·5). Note that the deeply concave, oval facet occupies the entire height of the nodal. (This picture is upside down with respect to conventional orientation.) 4, lateral view to show keeled and ornamented latera (× 10). Note the relatively low columnals and that the nodal is only about twice the height of the supranodal.

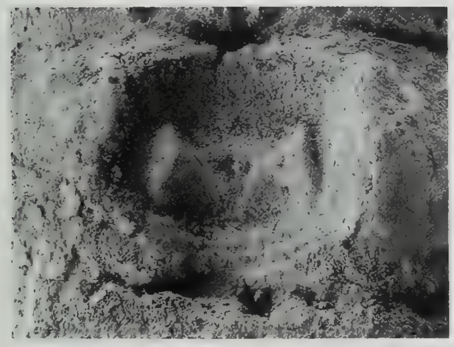
Figs 5–7 E.69673, somewhat atypical pluricolumnal resembling *?I neuvillensis* Valette, which Rasmussen (1961) regarded as a junior synonym of *?I. cenomanensis*: 5, detail of cirral facet (× 25). 6, detail of ornament on latera (× 25). 7, lateral view (× 8·5). Note that both nodals and internodals are proportionately higher and have weaker keels than is typical for *?I. cenomanensis*.

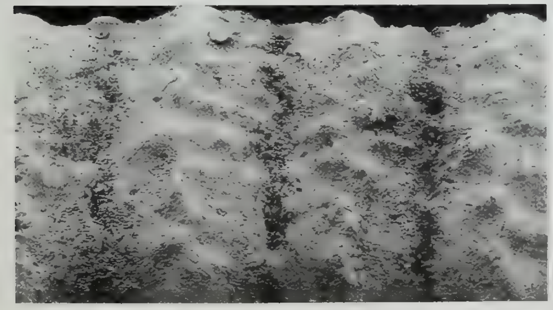

1

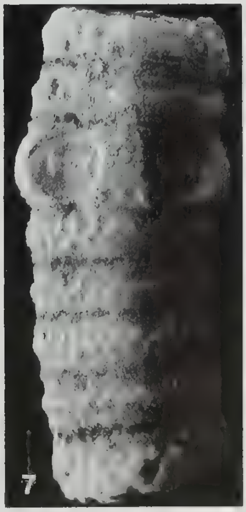

2


3


4


5


6


7

Nodals reach 6·5 mm in diameter, are thin (KH : KD averages 0·36) and have deeply concave cirral facets (facet concavity = 17–27%) which gives them a scalloped outline in cross section, particularly as the cirral facets usually occupy the entire height of the nodals (Pl. 44, fig. 3). Cirral facets are very slightly directed upwards (α ranges from 80–89°); nevertheless the profile of the latus is strongly convex and the widest part is just below mid-height (Pl. 44, fig. 4). Cirral facets are markedly oval (FH : FW ranges from 0·24–0·80) and separated from each other by narrow bands of latus about $\frac{1}{4}$ the width of the facets themselves. As in all isocrinids the proximal facet is symplectial and the distal cryptosymplectial. In *?I. cenomanensis* both facets are almost the same size. On the symplectial articulum, petals are narrow with 12–14 relatively long crenellae each, open at the periphery, and the most peripheral crenellae lie at 40–60° to the radius.

Internodals are of at least three orders which differ slightly in height and diameter. They reach 5·5 mm in diameter. Latera are distinctly keeled (Pl. 44, fig. 4), strongly convex (latus index varies from 23·5 to 37·5%) and covered with an irregular ornament of ridges and granules. Articulation facets are usually angularly pentalobate (Pl. 44, fig. 2). Areolae are relatively narrow and usually open. The lumen is pentagonal or rounded and moderately small (0·18–0·22 mm across).

Three complete noditaxes are known, varying from a nodal plus seven internodals to a nodal plus ten internodals. This variation is not entirely on account of growth. Specimen E.69642 bears canaliculi and hence is from the proximal stem: it has nine columnals in a complete noditaxis. However, E.69656 is from the distal stem and has only eight columnals in a complete noditaxis. E.69652 is from the distal stem and has eleven columnals in a complete noditaxis. Finally, E.69651 is a pluricolumnal of nine internodals; the cryptosymplectial articulation of the infranodal bears canaliculi so it must have come from the proximal stem. One can only conclude that complete noditaxes vary at least from nine to ten columnals in the proximal stem and at least from eight to eleven in the distal stem. A regular pattern of internodal orders is very difficult to make out as they differ only slightly in diameter and height. Nodals and internodals of the same stem vary in dimensions slightly. The nodal index ranges from 1·07–1·17 for diameter and 1·28–2·27 for height.

Cirri are unknown, but a single cirral plate occurs on E.69652 (Fig. 77C). The latus of this cirral bears a weak ornament of irregular granules much like that on the latera of columnals. Cirral facets are very strongly concave, only slightly angled upwards and very distinctly oval. The lumen of the cirri lies just above mid-height and is keyhole-shaped. The synarthrial ridges on either side of the lumen are almost symmetrical.

No cup or arm plates are known.

REMARKS. *?I. cenomanensis* is a distinctive species easy to separate from the other, commoner isocrinid at Wilmington. There is relatively little variation among specimens, although a few examples with higher columnals, weaker keels and more rounded cirral facets on the nodals occur (e.g. Pl. 44, figs 5–7); one of these (E.69672) was *in situ* near the top of the stratigraphical range of *?I. cenomanensis.* They resemble Valette's species *?I. neuvillensis*, which Rasmussen (1961: 118) considered to be a junior synonym of *?I. cenomanensis.* Too few specimens are known to distinguish these as a separate species or to be certain that they are confined to the upper part of the stratigraphical range. For the present all that can be done is to note that some atypical examples have been recorded.

?Isocrinus undulatus sp. nov.

Pls 45; 46; 47, figs 2, 4; 48, figs 1, 2, 4; Fig. 77A, B.

DIAGNOSIS. A species of *?Isocrinus* with thick columnals having smooth, rounded latera; articula with closed petals of 10–12 crenellae which continue regularly around the periphery so that the most distal crenellae parallel a radius. Nodals with almost planar, circular cirral facets which lie nearer the proximal articulum, occupy 60–88% of the nodal height and are directed up towards the cup. Nodals distinctly larger than internodals, which also vary significantly in both diameter and height. Noditaxis of at least 14 columnals.

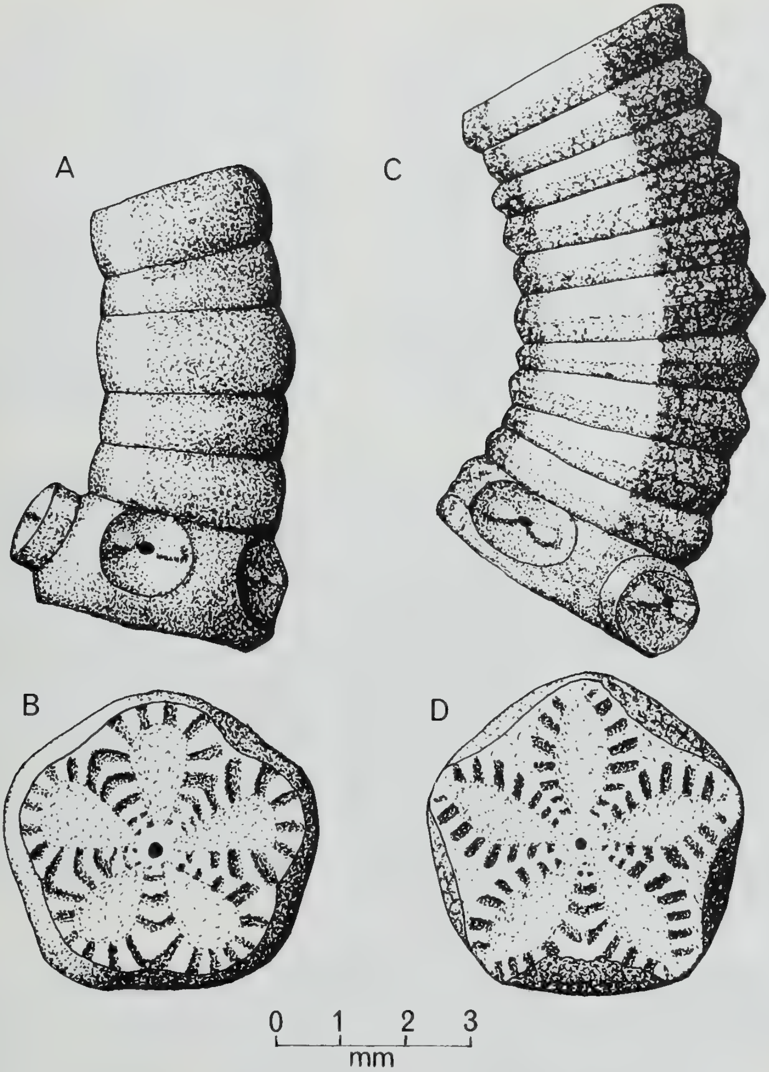


Fig. 77 Camera lucida drawings of pluricolumnals and articula of *?Isocrinus undulatus* sp. nov. (A–B) and *?Isocrinus cenomanensis* (d'Orbigny) (C–D) to show principal differences. A, **holotype** of *?I. undulatus* sp. nov., E.69700, a pluricolumnal consisting of a nodal bearing one cirral ossicle, the supranodal and four more internodals. Note the smooth rounded latera and almost circular cirral facets which do not occupy the full height of the nodal and are directed upwards. B, E.69702, the articulum of one internodal on a pluricolumnal consisting of three internodals. Note the closed petals. C, E.69652, a pluricolumnal showing a complete noditaxis and including a nodal with one cirral ossicle attached, and ten internodals. Note the thinner columnals with keeled and granular latera, and the oval cirral facets which are not directed upwards. D, E.69633, the articulum of one internodal on a pluricolumnal consisting of two internodals. Note the narrower, open petals and more angular outline. Collected *in situ* at 850 cm below datum level in the Wilmington Sands at the White Hart pit, Wilmington, Devon.

Holotype. BM(NH) E.69700 (Fig. 77A), a pluricolumnal consisting of five internodals above a nodal which bears a single cirral ossicle. Paratypes E.69680–99, E.69701–79, and E.69784–821.

Material. Several hundred columnals and pluricolumnals, of which 116 were *in situ* at Wilmington, and 15 radials, of which 7 were collected *in situ.* In addition, about 50 specimens including one radial have been collected *in situ* from the coastal sections near Beer Head.

Horizons. *?I. undulatus* ranges from 58 to 950 cm below datum at Wilmington, i.e. it is confined to the Cenomanian but ranges almost all the way through. On the coast we have collected it from 165 up to 480 cm above the Small Cove Hardground, i.e. in the Pounds Pool and Hooken Members of the Beer Head Limestone Formation. However, E.69701 was collected from the Little Beach Member at Humble Point, according to the label.

Description. *?I. undulatus* is known from stem fragments and radials only. The columnals are rounded to pentagonal in cross section, relatively thick, have smooth rounded convex latera and closed petals. The radials are massive, wedge-shaped ossicles.

Nodals (Pl. 45, fig. 3) reach 6·5 mm in diameter, have five nearly circular cirral facets (FH : FW ranges from 0·70 to 1·00) which are placed adjacent to the proximal (upper) articular facet and directed strongly upwards (α varies from 58–74°). Cirral facets are separated by narrow strips of latus about $\frac{1}{4}$ the width of the facets. The profile of the latus is strongly convex (latus index is 16–32%), but asymmetrical with the widest point well below mid-height. Cirral facets are weakly concave (never more than 10%) and occupy 58–88% of the nodal height. Mature nodals are thick (KH : KD averages 0·56) and the symplectial articulum is often significantly smaller than the cryptosymplectial.

Internodals are of four orders, which typically differ markedly in both diameter and height all along the stem (Pl. 45, fig. 5). The largest reach 6·0 mm in diameter. Latera are always smooth, although at very high magnifications an exceedingly fine granulation becomes apparent (Pl. 46, fig. 6). Latera vary from almost planar to strongly convex. Typically 4INN are the most nearly planar and convexity increases with internodal order. Articula (Pl. 45, fig. 1) are usually shallowly pentalobate and rounded, not angular, while the cross section of columnals is circular to rounded pentagonal. Articular facets have relatively broad areolae (Pl. 45, fig. 2) with 10–12 short crenellae each. The petals are closed and the crenellae continue regularly around the tips (Pl. 45, fig. 2) so that the most distal lie parallel to a radius ($\beta = 0°$). The lumen is round or pentagonal in cross section and very small (0·08–0·16 mm diameter).

No complete noditaxis is known, but it must include at least 14 columnals as E.69681 is a pluricolumnal composed of nodal and 12 internodals, apparently arranged 4342414342434. Nodals and internodals usually vary in diameter and height (Pl. 45, fig. 5), in which case the latera are also strongly convex. Some examples are known in which the internodals do not vary much in diameter and in these the latera are usually almost planar (e.g. Pl. 47, fig. 4). Nodal index (diameter) is 1·26–1·36; for height it is 1·30–3·91, but only rarely lies below 2·0.

No cirri have been found, but cirral plates are preserved on a few pluricolumnals. E.69680 bears two cirrals, while the holotype E.69700 (Fig. 77A) and E.69682 each bear a single cirral.

Plate 45

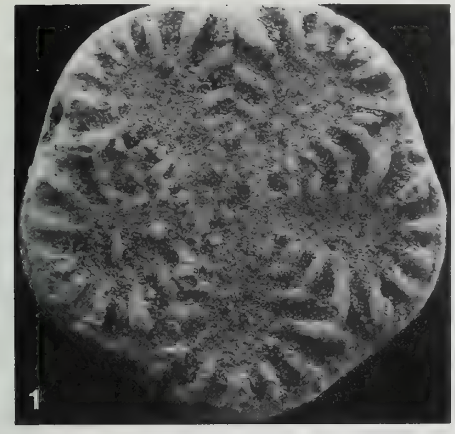
?Isocrinus undulatus sp. nov.

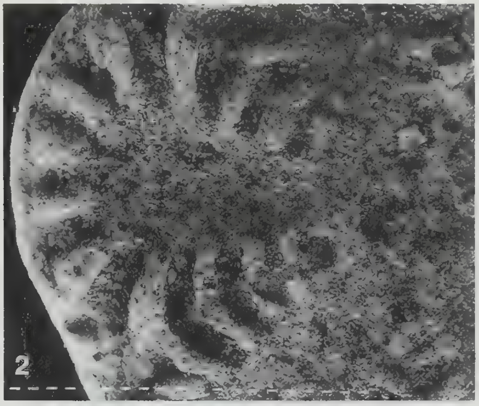
Figs 1, 2 E.69691, isolated internodal: 1, articulum (×11). 2, detail of one petal (×20). Note the wide, closed petal with peripheral crenellae parallel to the radius.

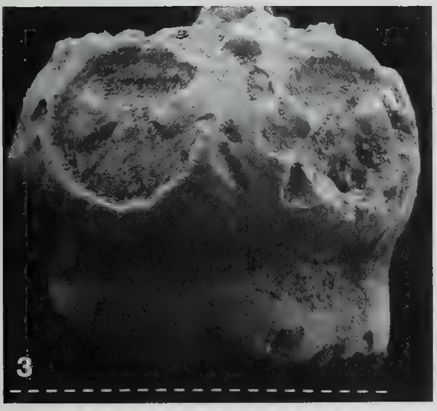
Fig. 3 E.69695, lateral view of a pluricolumnal which consists of a nodal and the infranodal below (×15). Note the relatively high columnals and the differences in dimensions of the nodal and infranodal; also that the nearly circular, relatively planar cirral facets are positioned near the upper margin of the nodal and directed upwards.

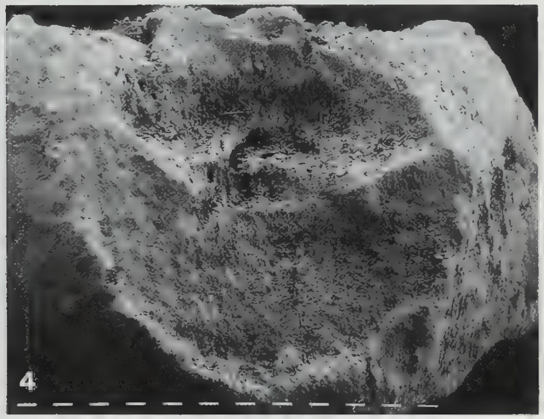
Fig. 4 E.69694, detail of the cirral facet on an isolated nodal (×25).

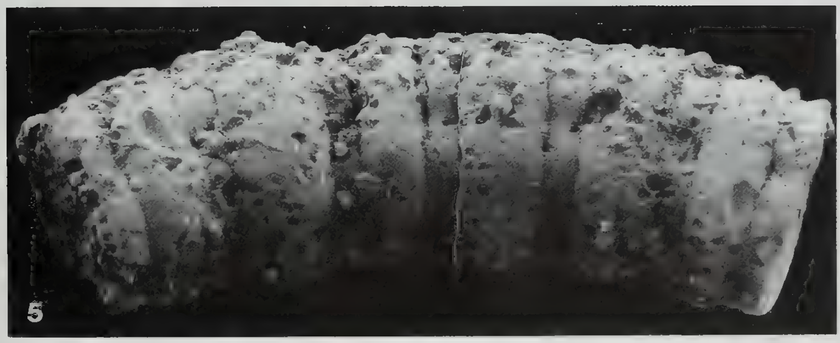
Fig. 5 E.69693, lateral view of a long pluricolumnal consisting of 13 internodals (×7·6). Note the smooth, convex latera (where not damaged by sand pitting) and differences in dimensions of the different orders of internodal. The order appears to be, from left to right, 4341434243434, in Webster's (1974) notation. See also Pl. 46, fig. 6.


1


2


3


4


5

Cirral facets are almost circular (Pl. 45, fig. 4), well above the midline of the nodals (Pl. 45, fig. 3), and are directed up towards the cup. In E.69680 the stump of the cirrus lies at 64° to the stem axis. Cirral facets are planar to weakly concave (0–10%) as seen in plan view of the nodal, and bear two short triangular synarthrial ridges laterally on either side of the cirral lumen which is just above mid height of the facet. The synarthrial ridge divides the facet into two ligament pits of which the upper is usually deeper and more concave. The cirral lumen is oval and small. Proximal cirrals are oval in cross section, thin (CH : CD is approximately 0·5), and have smooth latera.

Radials (Pl. 46, figs 1–5) are large, solid, wedge-shaped plates. They have two large lateral facets where they were in contact with adjacent radials (Pl. 46, fig. 2), a depressed crescentic brachial facet where they articulated with the first primibrach (Pl. 46, fig. 4), and two very small facets basally (Pl. 46, fig. 3 below) where they abutted against the basals. The internal edges of the radial : radial facets are straight, the remaining border is curved and bears traces of radiating crenellae (Pl. 46, figs 1–3). The brachial facet is almost horizontal, and usually lies between 80° and 89° to the axis, but rare examples have lower values. It has a nearly central transverse synarthrial ridge, external to which is a small oval nerve canal and a large semicircular dorsal ligament pit. Internal to the ridge is a shallow triangular depression with a central food groove that connects to the groove along the narrow internal edge adjacent to the body cavity. Basal facets are tiny and reach only about halfway to the outer face of the radials. The outline of the cup must have been distinctly stepped and the profile of several radials is undercut where it approaches the basal facets (e.g. Pl. 46, fig. 1). The external surfaces of available radials are smooth. This, together with the stratigraphical occurrence where columnals of *?I. undulatus* are commonest, strongly suggests these isolated radials derived from the same species. Radials vary significantly in height and width.

REMARKS. *?I. undulatus* is the most common species of crinoid at Wilmington and it is surprising that it has not been described before. It resembles the Albian species *?I. cretaceus*, but differs in having the cirral facets directed up not down, and in having a greater variation in the dimensions of internodals. We have examined several hundred nodals of *?I. undulatus* which without exception had the cirral facets facing upwards. In contrast, all the nodals of *?I. cretaceus* from the Gault Clay that we have seen had the cirral facets facing down. We have seen no examples with cirral facets at intermediate orientations and as the samples of both forms came from all parts of the stem, we believe they represent two distinct species. As with *?I. cenomanensis*, towards the top of the stratigraphical range atypical examples with more uniform columnals appear. The most extreme example, E.69698, a pluricolumnal of 8 internodals, is illustrated in Pl. 47, fig. 4. In this example, which was collected *in situ* at 87 cm below datum, columnal diameter remains constant, height varies slightly and latera are almost planar. Surface ornament (Pl. 47, fig. 2) and petals on the best-preserved articulum of E.69699 (Pl. 48, figs 1, 4) are typical of *?I. undulatus*; however, the latter example has completely smooth latera (Pl. 47, fig. 3). For the present we are including these specimens in *?I. undulatus*. It is possible that these specimens are transitional to the Turonian species *?I. granosus* Valette, which has similar articula to *?I. undulatus* and lateral ornament varying from smooth to densely granulated and keeled. These specimens should be considered with the next species.

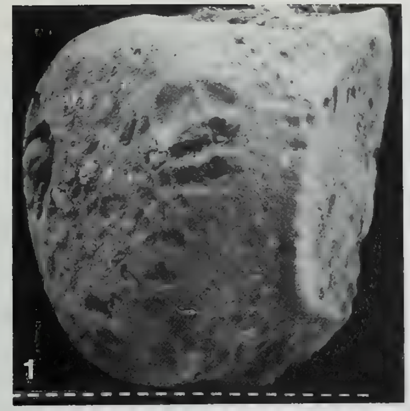
Plate 46

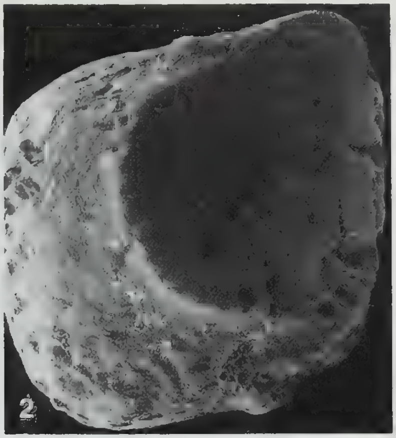
?Isocrinus undulatus sp. nov.

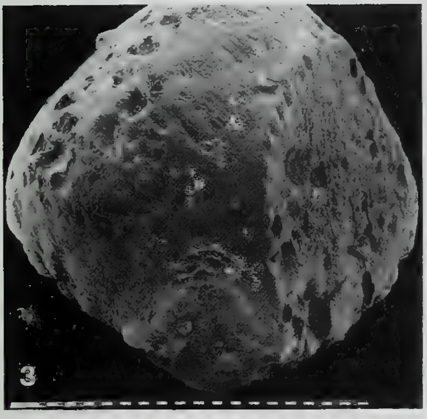
Figs 1–4 E.69696, isolated, relatively short and fat, radial plate: 1, oblique lateral view of external surface. 2, lateral view of radial : radial facet. Note weak crenellae. 3, oblique basal view. Note the very small radial : basal facet below. 4, ventral view of brachial facet. Note food groove (left). (All × 12·5).

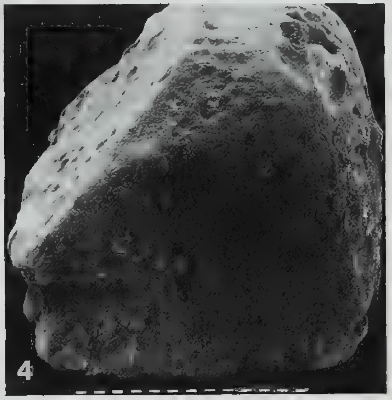
Fig. 5 E.69697, oblique lateral view of the external surface and radial : radial facet of an isolated, relatively tall and thin radial plate (× 9).

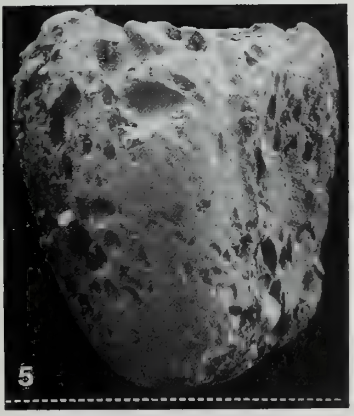
Fig. 6 E.69693, detail of surface ornament on one internodal (× 95). See also Pl. 45, fig. 5.

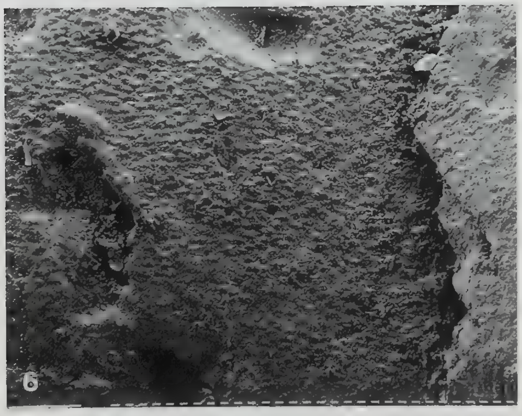

1


2


3


4


5


6

?Isocrinus cf. ***granosus*** Valette 1917

Pl. 47, figs 1, 5; Pl. 48, fig. 3

REMARKS. Rasmussen (1961: 130) gave a full synonymy for Valette's species. He included several synonyms and regarded *?I. granosus* as the only known Turonian isocrinid. A solitary loose pluricolumnal from Wilmington agrees most closely with the lectotype of *?I. granosus*, but differs from all known Cretaceous isocrinids in having lateral ornament of irregular ridges which are predominantly vertical. The uniqueness and poor preservation of the specimen preclude describing a new species.

MATERIAL. A single pluricolumnal of eight columnals, E.69660.

HORIZON. The specimen was collected loose, but the chalky, glauconitic matrix suggests that it came from the Wilmington Limestone.

DESCRIPTION. The nodal (Pl. 47, fig. 1 below) is stellate in outline, 3·9 mm across, with five deeply sunken cirral facets (Pl. 47, fig. 5) that are markedly concave both horizontally and vertically. The facets are central in the latus and occupy 100% of the nodal height. Between the cirral facets small areas of latus, which are planar (i.e. convexity = 0%) and ornamented with irregular vertical ridges, occur. Cirral facets are directed upwards very slightly. The cryptosymplectial articulum reveals a very small lumen; the nature of the symplectial articulum is unknown. The nodal is moderately thick (KH : KD = 0·43).

Internodals are rounded pentagonal in cross section, but otherwise almost identical in both height and diameter to each other and to the nodal, so their order is unknown. All have planar latera (Pl. 47, fig. 1) ornamented with irregular vertical ribs (Pl. 48, fig. 3). The exposed symplectial articulum is damaged by sand pitting so its characteristics remain unknown.

The single pluricolumnal does not preserve a complete noditaxis, but it must have included at least 8 columnals.

Cirri are unknown; however the cirral facets are deeply sunken into the nodal. The articulation fulcra have horizontal lower, and inclined upper, margins. The upper ligament pit is slightly deeper, but the supranodal bears no impression of the cirri, which apparently could not fold against the stem.

Order **COMATULIDA** Clark, 1908

DIAGNOSIS. Articular crinoids which as adults are usually free-living and have a large cirriferous centrodorsal plate set immediately below the cryptodicyclic cup.

REMARKS. Comatulids differ from other stemless crinoids, such as *Marsupites*, *Uintocrinus* and the roveacrinids, in having a large cirriferous centrodorsal plate.

Plate 47

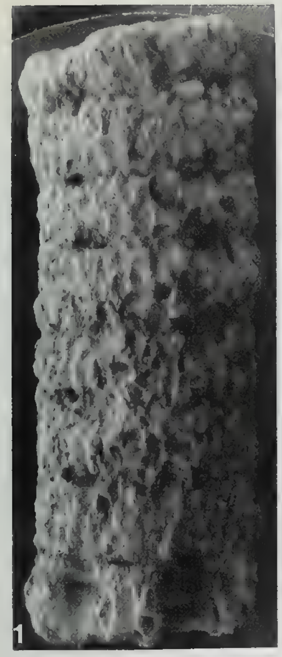
?Isocrinus cf. *granosus* Valette

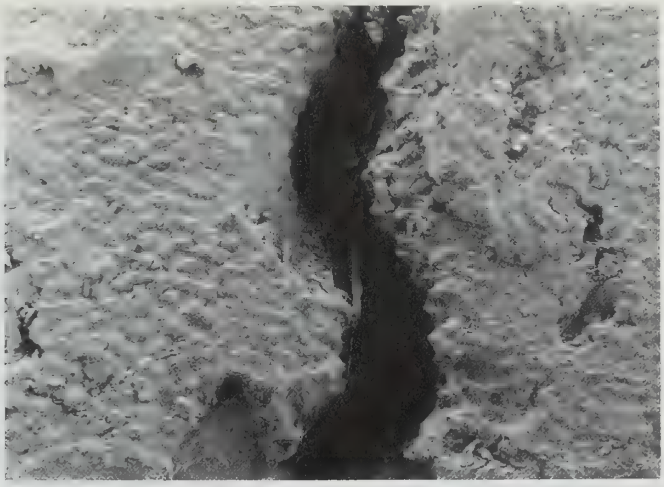
Figs 1, 5 E.69660, pluricolumnal consisting of a nodal and seven internodals: 1, lateral view to show deep, concave cirral facets and ornament of irregular vertical ridges on latera of internodals (× 8·5). 5, detail of cirral facet (× 35); this picture is upside down with respect to conventional orientation. See also Pl. 48, fig. 3.

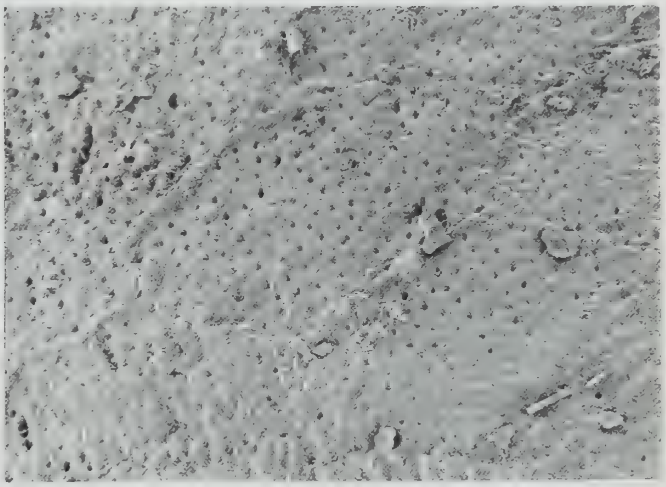
?Isocrinus undulatus sp. nov.

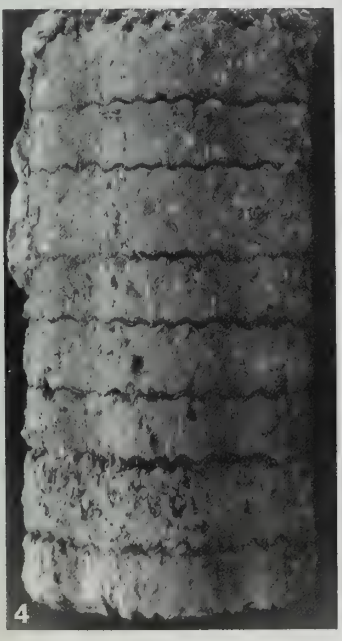
Figs 2, 4 E.69698, somewhat atypical pluricolumnal of eight internodals which have almost planar latera and very similar dimensions: 2, detail of surface ornament (× 130); compare Pl. 46, fig. 6. 4, lateral view (× 8·5). Collected *in situ* at 87 cm below datum, in the Wilmington limestone, Wilmington.

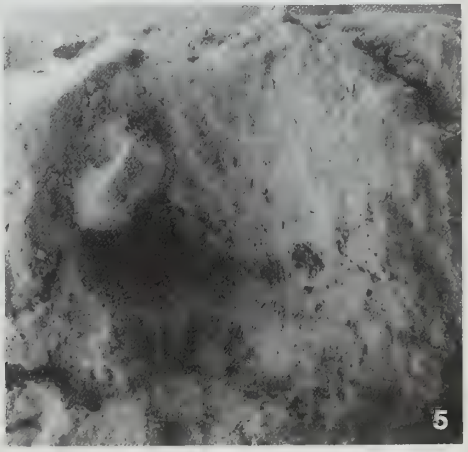
Fig. 3 E.69699, detail of stereom on the latus of an atypical pluricolumnal which consists of two internodals with planar latera (× 130). The weak diamond-shaped pattern is the remains of zooecial walls of an encrusting bryozoan colony. Collected *in situ* at 55 cm below datum, in the Wilmington limestone, Wilmington. See also Pl. 48, figs 1, 2, 4.


1


2


3


4


5

Superfamily **NOTOCRINACEA** Mortensen, 1918

Diagnosis. Comatulids with a centrodorsal composed of a single columnal having a cirrus-free dorsal area, which usually bears a dorsal star with the lobes in a radial position, or five radial pits.

Remarks. The solitary Recent genus *Aporometra* Clark, 1908, which has no dorsal star but a spongy calcareous structure dorsally on the centrodorsal instead, is placed in a separate family of its own. All other genera are placed in the family Notocrinidae which shares the characters of the superfamily, except that *Schlueterometra* lacks dorsal pits.

Family **NOTOCRINIDAE** Mortensen, 1918

Remarks. Rasmussen (1961: 278) suggested that *Remesimetra* Sieverts-Doreck should be regarded as a subgenus of *Glenotremites*. It differs principally in having a lower and more discoidal centrodorsal. However, he later (*in* Rasmussen & Sieverts-Doreck 1978: T904) accepted *Remesimetra* as a distinct genus. Material from Wilmington suggests that the distinction is rather arbitrary. *Loriolometra* also has a dorsal star in its conical centrodorsal, but never has more than 10 columns of cirri. Of the other genera included in the family Notocrinidae, *Schlueterometra* has no dorsal pits in its centrodorsal, while the Recent genus *Notocrinus* has six and the fossil genus *Semiometra* has five pits. They also differ in that the centrodorsal is conical with 10 columns of cirri in the former and discoidal with up to 20 irregular columns in the latter. These differences are summarized in the following artificial key.

Key to the genera of Notocrinidae

1.	Centrodorsal with dorsal star or radial pits	2
	Centrodorsal without dorsal star	***Schlueterometra***
2.	Centrodorsal with five radial pits dorsally	3
	Centrodorsal with stellate pit dorsally	4
3.	Centrodorsal conical, few cirri	***Notocrinus***
	Centrodorsal disc-shaped, many cirri	***Semiometra***
4.	Centrodorsal with 10 columns of cirri	***Loriolometra***
	Centrodorsal with 20 irregular columns of cirri	5
5.	Centrodorsal conical–hemispherical	***Glenotremites***
	Centrodorsal disc-shaped	***Remesimetra***

The fauna at Wilmington contains representatives of the genus *Glenotremites* (including *Remesimetra*), although some specimens show affinities with the genus *Semiometra*.

Genus ***GLENOTREMITES*** Goldfuss, 1829

Diagnosis. A genus of Notocrinidae in which the conical to hemispherical centrodorsal bears a dorsal star, and abundant cirri arranged in up to 20 irregular vertical columns.

Type species. *Glenotremites paradoxus* Goldfuss, 1829, by monotypy.

Other species. *G. aequimarginatus* (Carpenter, 1880*a*); *G. carentonensis* (de Loriol, 1894); *G. discoidalis* Gislén, 1925; *G. rotundus* (Carpenter, 1880*a*); *G. schlueterianus* Geinitz, 1871; *G. tourtiae* (Schlüter, 1878); *G. valettei* Gislén, 1924; *G. dondeyi* Girod, 1964 and *G. loveni* Ras-

---

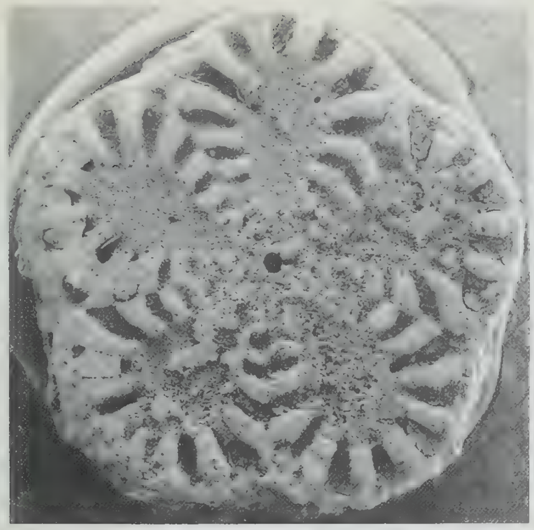
Plate 48

?Isocrinus undulatus sp. nov.

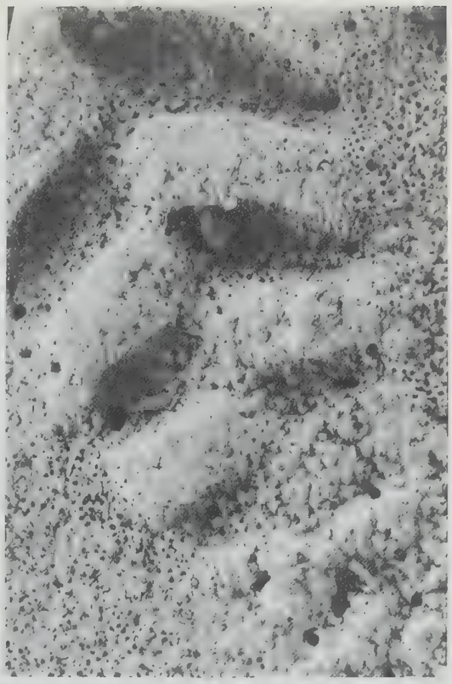
Figs 1, 2, 4 E.69699, atypical pluricolumnal of two internodals with planar latera: 1, well-preserved articulum (× 15). 2, detail of crenellae (× 70). Note the tubuli near the margins of the crenellae. 4, detail of one petal to show similarity to those typical of *?I. undulatus* sp. nov.; compare Pl. 45, fig. 1 (× 35). Collected *in situ* at 55 cm below datum, in the Wilmington limestone, Wilmington. See also Pl. 47, fig. 3.

?Isocrinus cf. *granosus* Valette

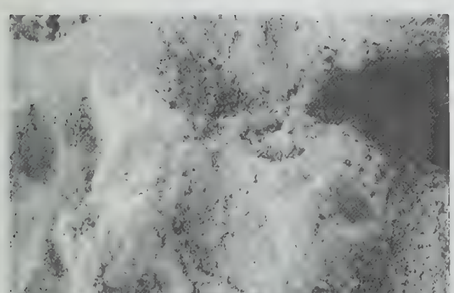
Fig. 3 E.69660, detail of ornament on latus (× 70). See also Pl. 47, figs 1, 5.



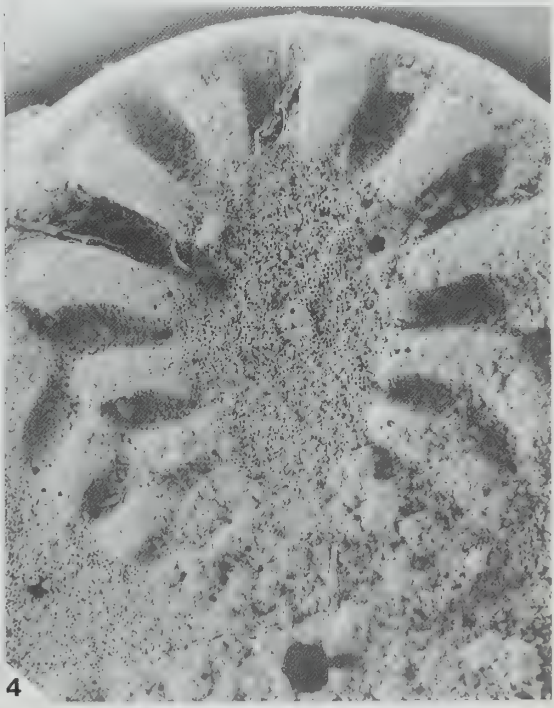
1



2



3



4

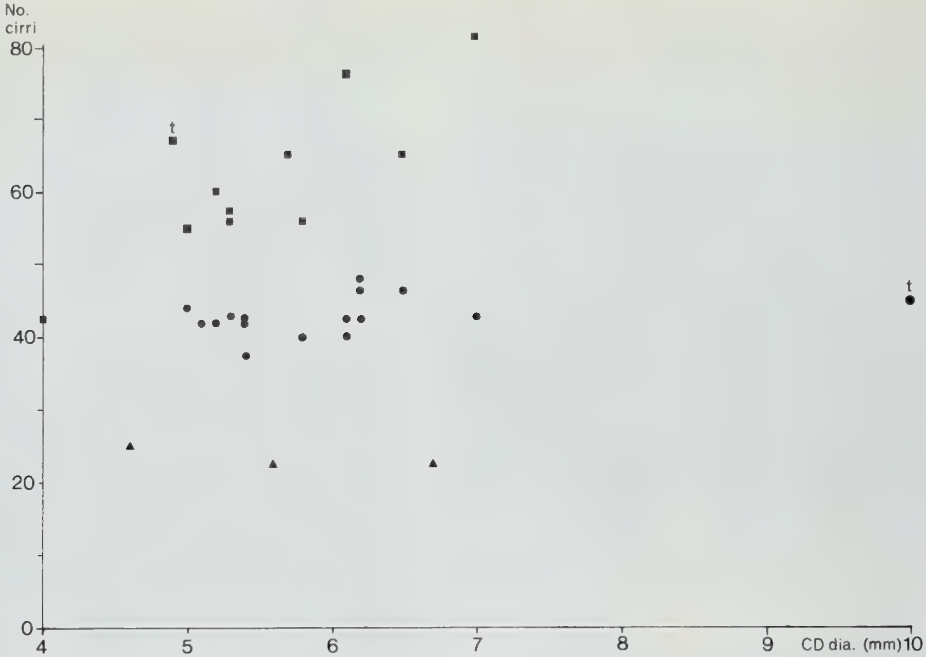


Fig. 78 Graph showing the relationship between the total number of cirri and the diameter of the centrodorsal plate in specimens of *Glenotremities*. ■ = *G. rotundus* (Carpenter), ● = *G.* cf. *aequimarginatus* (Carpenter), ▲ = *G.* cf. *paradoxus* Goldfuss. Larger symbols indicate examples from the Albian; t indicates the holotype of *G. rotundus* and *G. aequimarginatus*. Note the almost complete separation between the groups.

mussen, 1971. *G.* sp. of Pisera, 1983, also appears to be distinct. Rasmussen (1961: 279) published a key to all the then known species.

Remarks. The comatulid fauna at Wilmington consists of isolated cups or centrodorsals which reveal few of the characters on which species of Recent crinoids are distinguished. Sand pitting of surfaces further increases this difficulty. Nevertheless, the fauna at Wilmington does include a reasonable number of specimens from a relatively restricted stratigraphical interval and so gives an idea of variation at one locality and time. Most fossil comatulids are known from rare specimens or samples from widely scattered geographical localities and stratigraphical intervals. A graph of the diameter of the centrodorsal against total number of cirri (Fig. 78) reveals three almost totally exclusive groups. Other characters do not provide quite such a clear cut separation (e.g. Fig. 79), but do tend to confirm that more than one species is present at Wilmington. The group with the highest number of cirri includes the holotype of *G. rotundus* (Carpenter). Apparently in this species cirri were added rapidly throughout growth, the total number varying from about 40 at 4 mm diameter to over 80 at 7 mm diameter. Specimens in this group tend to have a relatively small dorsal star closely surrounded by cirral facets (Fig. 75A) and they tend to have relatively low centrodorsals.

The group with intermediate numbers of cirri apparently added almost all cirri before reaching 5 mm diameter and then did not add any more. The total varies from about 38 to 48 between 5 and 7 mm diameter. The holotype of *G. aequimarginatus* (Carpenter), a large cup 10 mm in diameter, has 45 cirral facets and resembles the Wilmington specimens quite closely. The slight differences could be due to the larger size and better preservation of the specimen from the Gault Clay. Provisionally the Wilmington group of specimens is referred to *G.* cf. *aequimarginatus*. It includes specimens with a relatively large dorsal star surrounded by a cirrus-free zone and a centrodorsal which is relatively high. The dorsal star varies from a

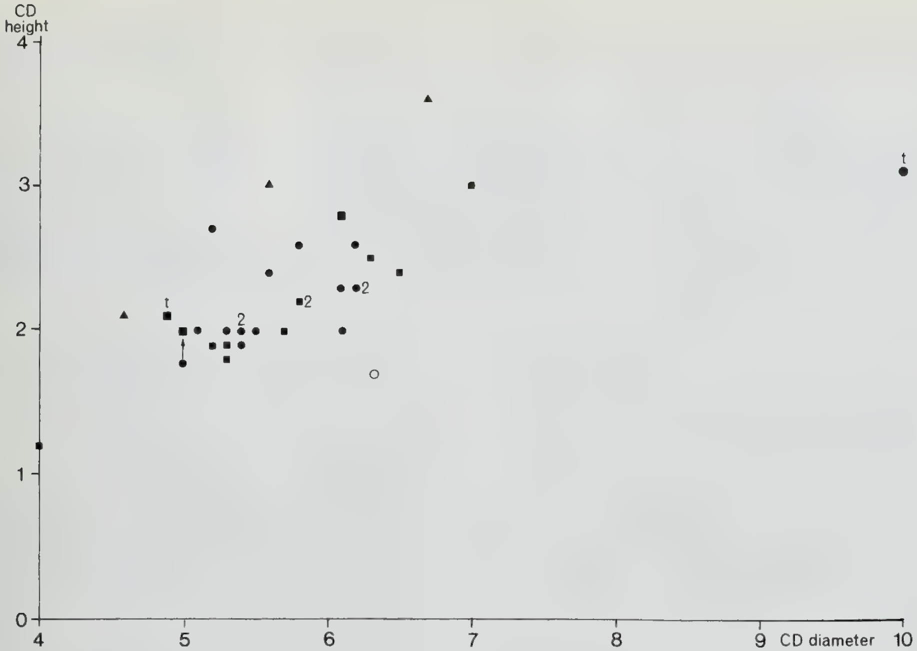


Fig. 79 Graph showing the relationship between height and diameter of the centrodorsal plates in specimens of *Glenotremites*. Symbols as in Fig. 78. Note the poor separation. However, most of the Cenomanian specimens of *G. rotundus* (■) lie towards the lower edge of the scatter (although the Albian examples have consistently higher centrodorsals) and all three examples of *G.* cf. *paradoxus* (▲) lie along the upper margin of the scatter. (○) *G.* cf. *discoidalis* Gislén.

five-rayed pit typical of *Glenotremites* (Pl. 50, fig. 5; Pl. 51, fig. 8), through a five-rayed pit with a raised central area and deeper rays (Pl. 49, figs 3, 4), to five completely separate pits (Pl. 49, figs 1, 5). The latter arrangement is characteristic of the genus *Semiometra*, but we believe that all these Wilmington specimens belong to a single species. True *Semiometra* has a much lower, saucer-shaped, centrodorsal.

The group with the lowest number of cirral facets includes only three specimens, all of which are rather poorly preserved centrodorsals. The best-preserved strongly resembles the type of *G. paradoxus* Goldfuss from the Cenomanian or Turonian of Germany. Provisionally these three specimens are referred to *G.* cf. *paradoxus*. They tend to have very high centrodorsals and cirral facets which vary widely in diameter.

Finally, specimen E.69470 (Fig. 80A, B) is a very badly preserved cup in which it is impossible even to estimate the total number of cirral facets. It differs from all the other specimens in having a very wide, flat dorsal area free of cirral facets in which there is a weak radial dorsal star and some even weaker interradial depressions as well. This specimen is referred to *G.* cf. *discoidalis* Gislén, the type of which came from the Cenomanian of Czechoslovakia.

Glenotremites rotundus (Carpenter 1880)

Pl. 50, fig. 4; Pl. 51, fig. 7.

1880*a* *Antedon rotunda* Carpenter: 52; pl. 5, figs 5a–c.
1880*b* *Antedon incurva* Carpenter: 552; pl. 23, figs 1a–d.
1924 *Glenotremites rotundus* (Carpenter) Gislén: 126, 136.
1924 *Sphaerometra incurva* (Carpenter) Gislén: 169, 170.
1925 *Glenotremites rotundus* (Carpenter); Gislén: 2, 19, 28; figs 33–34.
1925 *Sphaerometra incurva* (Carpenter); Gislén: 18.
1961 *Glenotremites rotundus* (Carpenter); Rasmussen: 295; pl. 42, figs 1, 2a–c.

DIAGNOSIS. A species of *Glenotremites* with a rounded subconical to hemispherical centrodorsal, dorsal star surrounded by narrow cirrus-free area, cirral scars densely crowded, cirri added throughout growth, up to 82 in all.

HOLOTYPE. BM(NH) E.35620, from the Albian, Upper Greensand, at Haldon, Devon. (Holotype of *A. incurva*, BM(NH) E.6476, recorded in error as E.6475 by Rasmussen (1961: 296), from the Albian, Upper Greensand, of Blackdown, Devon.)

MATERIAL. Six cups (E.69478, E.69480–1, E.69489, E.69492 and E.69495) from Wilmington can definitely be assigned to this species and two more, E.69488 and E.69502, may belong here but are too badly coated for one to be certain. In addition E.67612–3, two complete cups collected by Greenaway, are assigned to this species. Rasmussen (1961: 296) noted a further centrodorsal from Wilmington in the collection of C. W. Wright (WW 15483). We have also been able to compare two isolated centrodorsals from the Albian, Blackdown Greensand of Blackdown, Devon, E.51656–7.

DESCRIPTION. Centrodorsal reaching 7 mm across, pentagonal to subcircular in outline, subconical to hemispherical in profile (Pl. 50, fig. 4). Basal cirrus-free area small, with a distinct, deep dorsal star (Fig. 75A). Cirral facets densely crowded, polygonal, irregular in arrangement with up to four in each radius and up to four vertically, increasing from about 40 at 4 mm diameter to about 80 at 7 mm diameter (Fig. 78). Each facet is deep, conical, with paired synarthrial ridges set horizontally on either side of the ?circular lumen (Pl. 51, fig. 7). Margins of cirral facets prominent, with radiating crenellae.

Ventral surface of centrodorsal is distinctly concave in the two Albian centrodorsals (Fig. 75B). The moderate-sized central cavity is surrounded by five radially positioned oval nerve canals. Five long, thin, shallow depressions for the basals are situated interradially and have prominent, smooth rims.

Basals are long, thin plates which apparently do not meet and are triangular in section. The tips are just visible laterally in complete cups. Radials are triangular in outline both vertically and horizontally, without free lateral faces. Only the interradial wings reach the margin of the centrodorsal. The brachial facet occupies the entire lateral surface (Pl. 50, fig. 4) and has a moderately long, deep dorsal ligament pit below the horizontal synarthrial ridge. Above these are two relatively shallow interarticular ligament pits and above them two prominent, deep ventral muscle pits. The food groove is a narrow cleft at the top leading into a moderate-sized body cavity which is circular in cross section.

Arms and cirri unknown.

REMARKS. *G. rotundus* is relatively rare at Wilmington. It appears to be characterized by a centrodorsal with a narrow cirrus-free area around the dorsal star and abundant cirri, more than in any other species, which were added throughout growth.

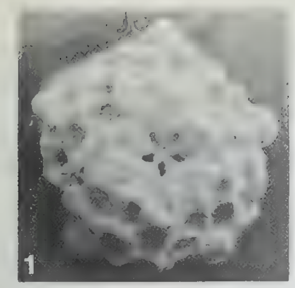
Plate 49

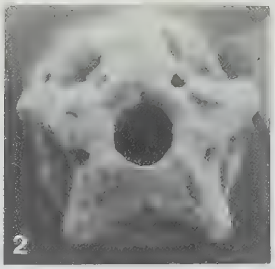
Glenotremites cf. *aequimarginatus* (Carpenter)

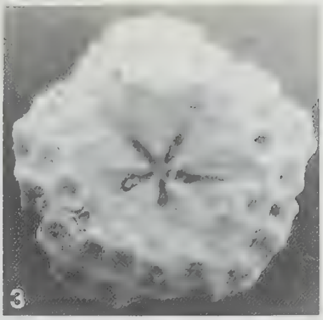
Figs 1, 2, 5, 7, 8 E.69800, complete cup with worn radials: 1, dorsal view to show five separate radial pits and deep cirral facets (× 6). 2, ventral view to show body cavity, worn radial crests and protruding radial wings (× 6). 5, detail of dorsal radial pits (× 24). 7, oblique lateral view to show brachial facet (× 12). Note the gaps between the radial and centrodorsal. 8, detail of radial nerve canal and dorsal ligament pit (below) (× 50).

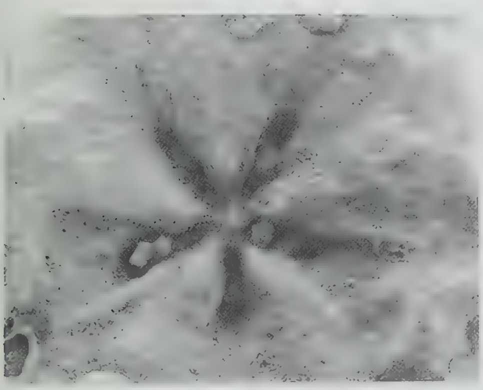
Figs 3, 4, 6 E.69802, complete cup. 3, dorsal view showing the dorsal star (× 6). 4, detail of dorsal star (× 12). Note that the radial pits are deeper than the centre of the star. 6, detail of one brachial facet (× 12). Note the food groove (above) and deep groove along the radial : radial suture (right).

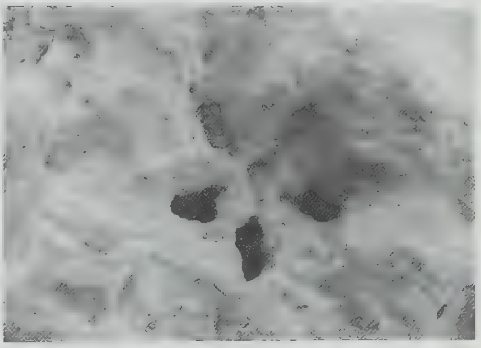
Fig. 9 E.69801, detail of one basal depression on the ventral surface of an isolated centrodorsal plate (× 24). Note the crenellae along the margin of the basal depression and the stereom structure (below).

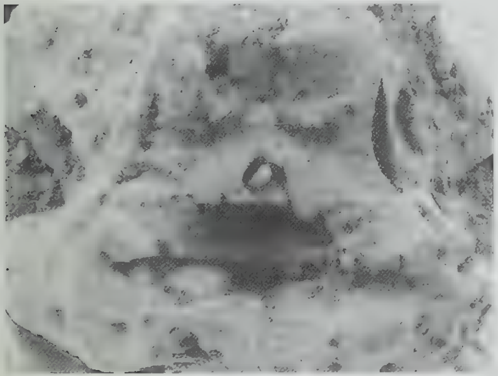

1

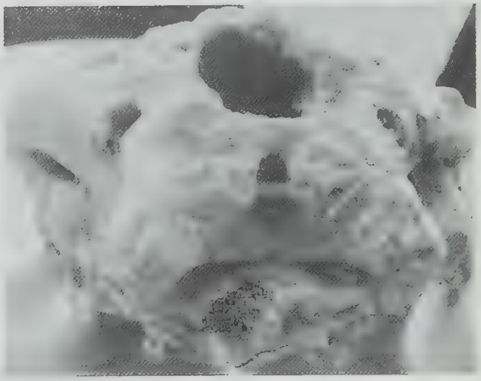

2

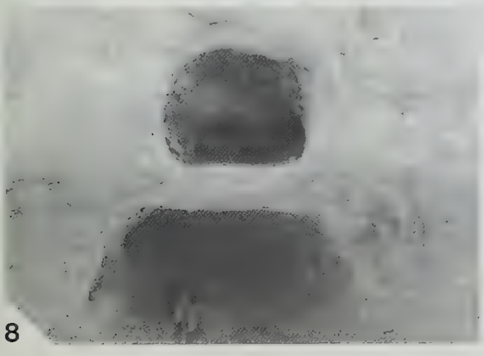

3

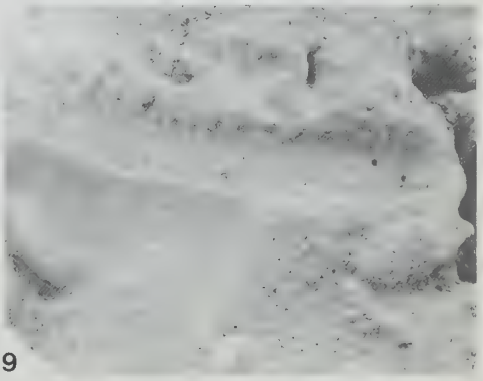

4


5


6


7


8


9

Glenotremites cf. ***aequimarginatus*** (Carpenter 1880)
Pl. 49; Pl. 50, figs 1–3, 5; Pl. 51, figs 1–5, 8, 9

1880*a* *Antedon aequimarginata* Carpenter: 49; pl. 5, fig. 4.
1924 *Sphaerometra aequimarginata* (Carpenter) Gislén: 169.
1961 *Glenotremites aequimarginatus* (Carpenter) Rasmussen: 280; pl. 41, fig. 1.

DIAGNOSIS. A species of *Glenotremites* with a hemispherical to almost discoidal centrodorsal, dorsal star surrounded by a relatively wide cirrus-free area, cirri apparently not added to during growth, crowded and arranged irregularly, up to four per radius and two to three vertically, 38–48 in all.

HOLOTYPE. BM(NH) E.40365, a complete cup, from the Gault Clay (Albian) of Folkestone, Kent. Hitherto the holotype was the only known specimen.

MATERIAL. Sixteen cups and centrodorsals (E.69471–7, E.69479, E.69482, E.69486, E.69490–1, E.69493–4, E.69503–4) can be fairly confidently assigned to this species and two more (E.69487, E.69505) are doubtfully included here. All but one were collected loose at Wilmington. In addition, E.69301, a centrodorsal collected by H. G. Owen, R. J. Cleevely and D. N. Lewis from 'sands about 25 feet below the grizzle', belongs to this species.

DESCRIPTION. Centrodorsal pentagonal in outline (Pl. 49, figs 1, 3; Pl. 50, fig. 5), hemispherical to disc-shaped in profile (Pl. 50, fig. 2). Dorsal star with deep narrow rays (Pl. 51, fig. 8) or five separate radial pits (Pl. 49, fig. 5), surrounded by a relatively broad cirrus-free area (Pl. 49, fig. 3). Cirral facets moderately densely crowded, polygonal, conical and moderately deep (Pl. 50, fig. 2). They reach 1 mm across, are irregularly arranged, have weak horizontal synarthrial ridges and fine crenellae around the margins (Pl. 51, fig. 4). Total 38–48, apparently not increasing in number over the size range available (Fig. 78). They vary from 42 or 43 at 5 mm diameter to 45 at 10 mm diameter in the holotype and never exceed 48.

Ventral surface of centrodorsal more or less flat with a deep central pit surrounded by the usual five radial nerve canals (Pl. 50, fig. 3). Grooves for basals shallow, relatively long and narrow and turning up at the periphery (Pl. 49, fig. 9). Rims indistinct and crenellate. Surface of radial areas uneven.

Basals are long, thin plates, triangular in section. They expand slightly centrally but do not meet. Only the tips are visible in complete cups (Pl. 51, fig. 5). Radials are triangular, without free lateral surfaces, and only reach the margin of the centrodorsal interradially (Pl. 49, fig. 2). Brachial facets with relatively long dorsal ligament pit below the synarthrial ridge (Pl. 49, fig. 6). Interarticular ligament pits triangular, ventral muscle pits moderately deep. The food groove is a narrow V-shaped notch. Below the radial crests the radial : radial sutures are obvious open grooves (Pl. 49, fig. 6 right), closing once shortly before revealing the basals peripherally. The top of the body cavity is wide and star-shaped.

Arms and cirri unknown.

REMARKS. This species is very similar to *G. rotundus*, but has a generally thicker centrodorsal which is flatter ventrally. The dorsal star is surrounded by a wider cirrus-free area and may have a raised central area or consist of five quite separate radial pits as in *Semiometra*. The centrodorsal is much higher than in typical *Semiometra*, however. There are fewer cirri than in *G. rotundus* and apparently none is added after the centrodorsal reaches about 5 mm diameter. This species has a dorsal star which varies from that typical of *Glenotremites* to that typical of *Semiometra*. The holotype of *G. aequimarginatus* is larger than any example from Wilmington and also stratigraphically older. It has a deep dorsal star, radial wings which do not protrude beyond the margin of the centrodorsal, and basals which are scarcely visible at all. With only the single specimen from the Gault Clay, it is not known how much these differences are ontogenetic in origin, or result from the different preservation and geological age. For the present it seems best to refer the Wilmington specimens to *G.* cf. *aequimarginatus*.

***Glenotremites* cf. *paradoxus* Goldfuss 1829**
Pl. 50, fig. 7.

1829 *Glenotremites paradoxus* Goldfuss: 159; pl. 49, fig. 9.
1831 *Glenotremites paradoxus* Goldfuss; Goldfuss: 168; pl. 51, fig. 1.
1961 *Glenotremites paradoxus* Goldfuss; Rasmussen: 284; pl. 39, figs 6a–c.
1978 *Glenotremites paradoxus* Goldfuss; Rasmussen (*in* Rasmussen & Sieverts-Doreck): T903, figs 602, 1d–e (?figs 1a–c, 1f–h.)

SYNONYMS. Rasmussen (1961: 284) listed 20 synonyms for this species, applied to specimens ranging in age from Cenomanian to Santonian and coming from Britain, France, Germany, Poland and Czechoslovakia. They include centrodorsals of a wide variety of shapes and sizes, some with a clear dorsal star, some with five radial pits (e.g. cf. Rasmussen, 1961: pl. 39, figs 6c and 7c). We believe that quite possibly more than one species is included in this form as understood by Rasmussen and here refer only to the holotype, which most closely resembles our specimens and may have come from a similar stratigraphical level.

DIAGNOSIS. A species of *Glenotremites* with a high, discoidal centrodorsal with a dorsal star (in the holotype). About 25 cirral facets, 3 per radius and 2 or 3 vertically. Cirri apparently not added during later growth, varying in size and relatively widely separated ventrally. Ventral surface of centrodorsal convex.

HOLOTYPE. In the collection of the Geologisch-Paläontologisches Institut der Universität, Bonn, West Germany. The specimen figured by Rasmussen (1961: pl. 39, figs 6a–c) is said by him (1961: 285) to be the holotype. It is from the Chalk Marl of Speldorf, between Duisburg and Mühlheim, West Germany. According to Rasmussen the adhering sediment is glauconitic sand, suggesting a Cenomanian or Turonian age.

MATERIAL. Three poorly preserved centrodorsals, of which E.69496 quite closely resembles the type. E.69483 and E.69500 are progressively less well preserved and their assignment to this species is less certain. All were collected loose at Wilmington.

DESCRIPTION. Centrodorsal relatively thick, height greater than 50% of diameter in E.69483 and E.69496. Deep dorsal pit more than 35% of the centrodorsal diameter, but with no clear dorsal star, in E.69496 and E.69500; dorsal surface coated in E.69483. Cirral facets rounded, reaching 1·2 mm across, shallow, smooth, apparently without synarthrial ridges or crenellae. No more than three per radius and only two vertically; estimated total about 25 in all three examples. Ventral surface of the centrodorsal convex, curving down laterally (Pl. 50, fig. 7 upper left) between widely spaced cirral facets. Depressions for basals raised above the irregular radial surfaces (Pl. 50, fig. 7). Ventral cavity about 25% of the diameter, with five radial nerve canals. One basal preserved in E.69483. It is triangular in section, elongate and raised peripherally.

No other features of cup, arms or cirri are known.

REMARKS. These three centrodorsals differ from all the other specimens from Wilmington in having fewer cirral facets, and these vary greatly in size, are shallow, smooth and apparently lack synarthrial ridges or crenellae. The ventral surface is irregular radially, convex and the centrodorsal proportionately higher than in the others. All three specimens are poorly preserved, but among described species, most closely resemble the type of *Glenotremites paradoxus*.

***Glenotremites* cf. *discoidalis* Gislén 1925**
Fig. 80A, B

1911 *Glenotremites rosaceus* Frič (*non* Geinitz): 77; figs 321, 1–3 (*non* 4).
1925 *Glenotremites discoidalis* Gislén: 10, figs 16–19.
1958 *Glenotremites discoidalis* Gislén; Sieverts-Doreck: 257; pl. 7, fig. 4; text-fig. 2.
1961 *Glenotremites discoidalis* Gislén; Rasmussen: 282; pl. 41, figs 3–4.

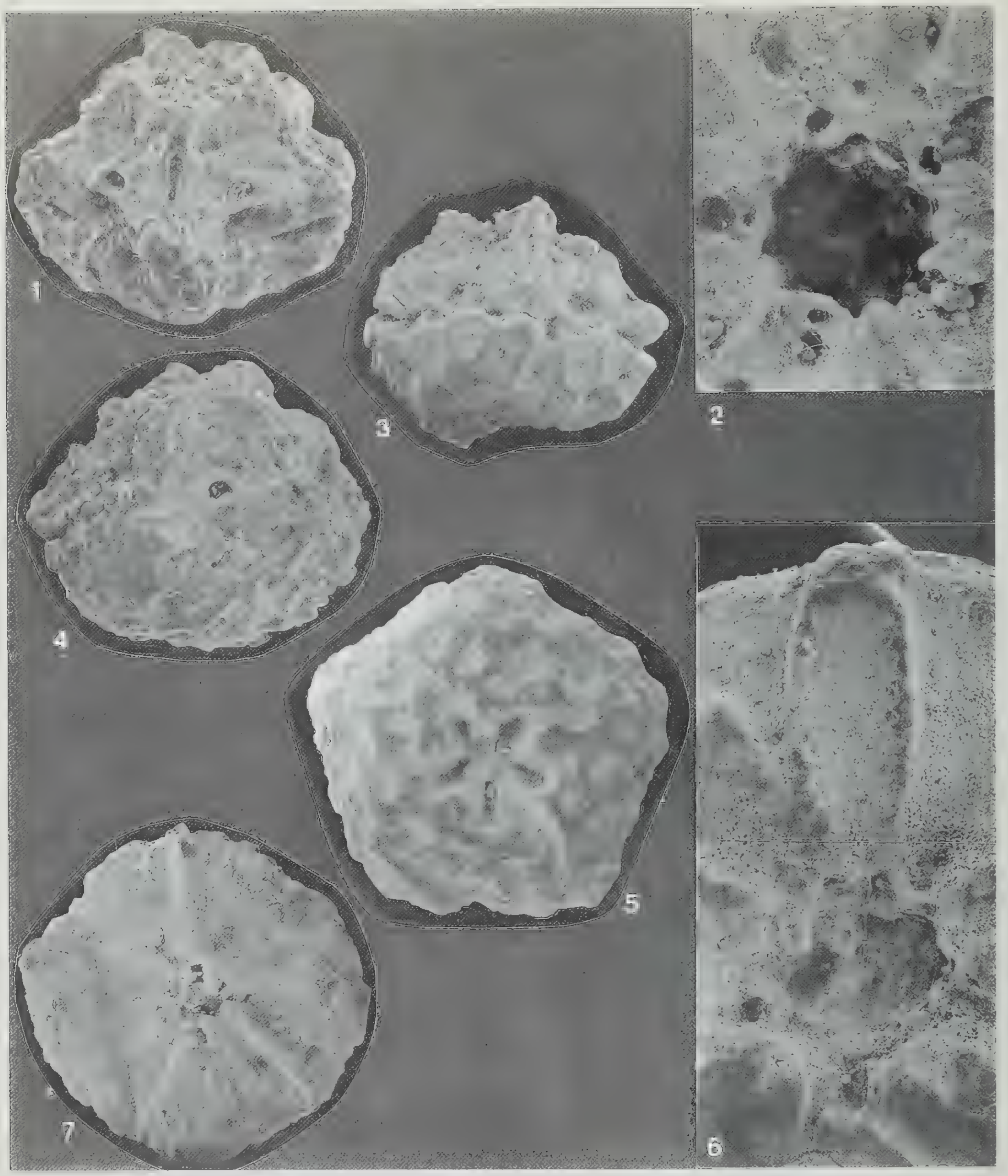


Plate 50

Glenotremites cf. *aequimarginatus* (Carpenter)

Fig. 1 E.69474, oblique lateral view centred on an interradius (×9·1). Note the deep groove along the radial : radial suture. See also Pl. 51, figs 1–3.

Fig. 2 E.69473, detail of the central cavity on the centrodorsal (×22). Note the radial nerve canals around the central cavity.

Fig. 3 E.69479, oblique view of centrodorsal showing the cirral facets (×8). See also Pl. 51, figs 4–5.

Fig. 5 E.69477, dorsal view of a centrodorsal showing a large dorsal star (×8). See also Pl. 51, fig. 8.

Glenotremites rotundus (Carpenter)

Fig. 4 E.69481, lateral view showing hemispherical profile of centrodorsal and well preserved brachial facet (×8·7).

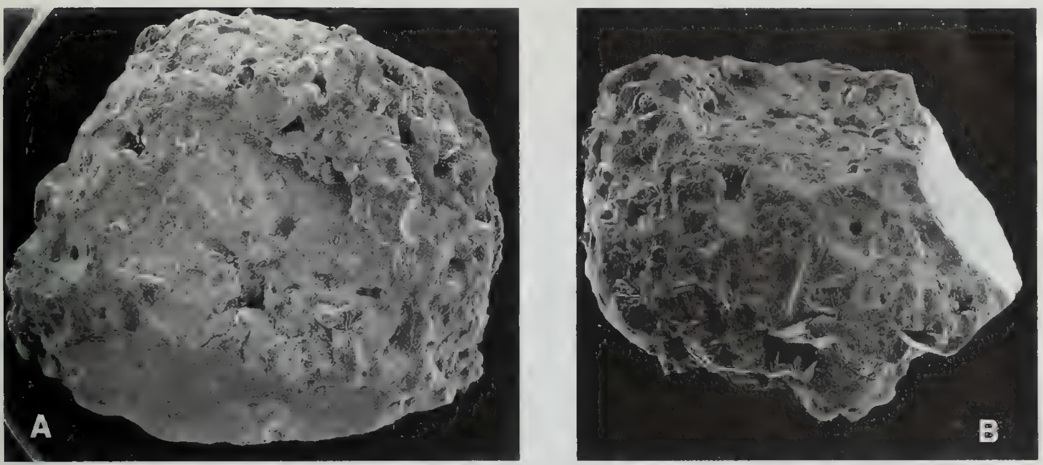


Fig. 80 *Glenotremites* cf. *discoidalis* Gislén. E.69470, poorly preserved theca. A, dorsal view of the centrodorsal to show the flat dorsal surface with a weak dorsal star (× 11·7); B, oblique view of centrodorsal showing one cirral facet (× 11·8) [specimen upside down with respect to conventional orientation].

Diagnosis. A species of *Glenotremites* with a discoidal centrodorsal with few cirri (about 25 in the holotype). Very large cirrus-free dorsal area with a radial dorsal star and weak interradial grooves as well. Ventral surface planar with elongate radial nerve canals.

Holotype. BM(NH) E.14895, an isolated centrodorsal from the Cenomanian of Kamajk, near Časlav, Czechoslovakia.

Material. One poorly preserved, damaged theca, E.69470, collected loose at Wilmington.

Description. Discoidal centrodorsal, 6·3 mm in diameter × 1·7 mm high, with shallow truncated conical profile. Flat dorsal surface with weak radial grooves, not forming a truly stellate pit, and weaker interradial impressions (Fig. 80A). Dorsal cirrus-free area very wide. Few cirral facets, possibly in a single row, but the centrodorsal is too badly damaged to estimate the total number. Cirral facets apparently bear synarthrial ridges and crenellae (Fig. 80B).

Radials poorly preserved; cup reaching 4·3 mm high, but worn ventrally. Other details not preserved.

Remarks. The specimen is very poorly preserved, but quite unlike any other from Wilmington with its very wide, flat dorsal area and very weak radial and interradial grooves. It resembles the holotype of *G. discoidalis*, but is too poorly preserved to be certain of this identification.

***Glenotremites* sp.**
Pl. 50, fig. 6; Pl. 51, fig. 6.

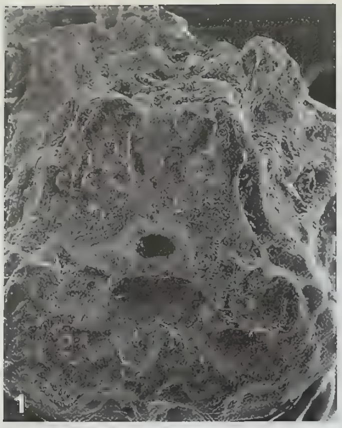
In addition to the specimens described above, a further seven poorly preserved cups and one centrodorsal have been collected loose at Wilmington. All are too badly preserved to be identified.

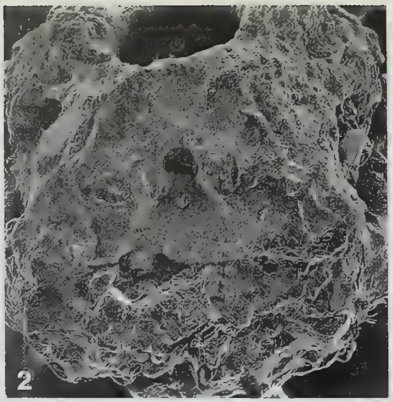
Glenotremites sp.

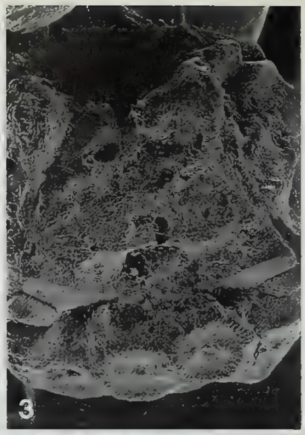
Fig. 6 E.69497, ventral view of an isolated centrodorsal with a single basal plate preserved (above) (× 8·8). Note the crenellae along the edge of the basal. See also Pl. 51, fig. 6.

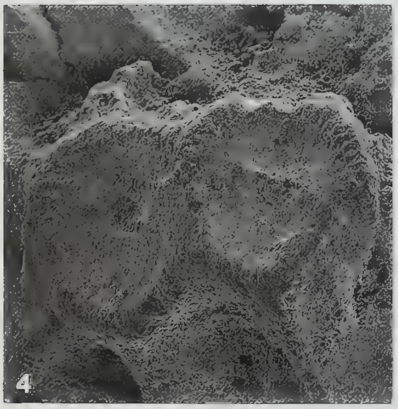
Glenotremites cf. *paradoxus* Goldfuss

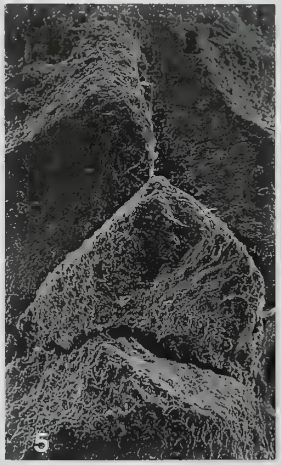
Fig. 7 E.69496, detail of the ventral cavity and one basal depression in an isolated centrodorsal plate (× 22). Note the crenellae along the edges of the basal depression and the cirral bud growing out beside it (above left).

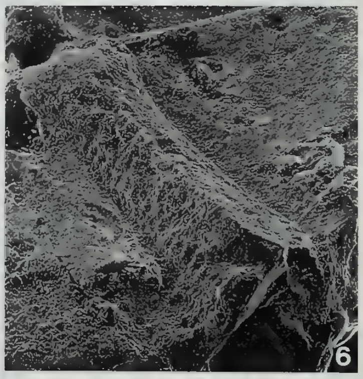


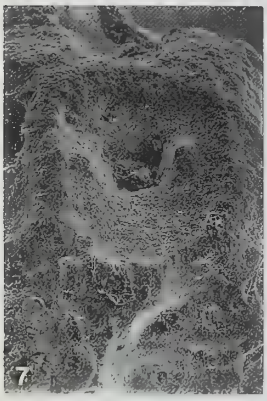


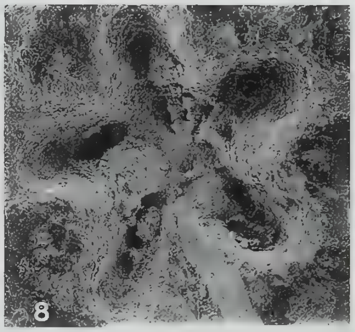












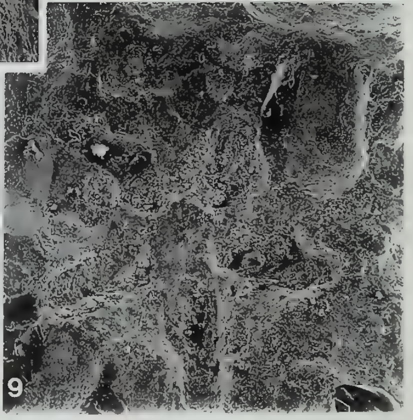


Plate 51

Glenotremites cf. *aequimarginatus* (Carpenter).

Figs 1–3 E.69474, details of three brachial facets (all × 12·1). Note cirral facets in 3 and food grooves (above) in 1 and 3. See also Pl. 50, fig. 1.

Figs 4–5 E.69479. 4, cirral facets on centrodorsal plate (× 30). 5, basal plate exposed between radial plates (× 35). See also Pl. 50, fig. 3.

Fig. 8 E.69477, detail of an unusually large dorsal star (× 19·3). See also Pl. 50, fig. 5.

Fig. 9 E.69476, detail of a shallow dorsal star (× 38·5).

Glenotremites sp.

Fig. 6 E.69497, detail of the single preserved basal plate (× 27·5). See also Pl. 50, fig. 6.

Glenotremites rotundus (Carpenter).

Fig. 7 E.69478, detail of cirral facets (× 33). Note the small synarthrial ridges on either side of the lumen and the peripheral crenellae.

Acknowledgements

The initial fieldwork that led to this project was undertaken by C.R.C.P. during the tenure of a Nuffield Foundation Science Fellowship. The basic work of collecting and recording specimens from the sections at Wilmington and the Devon coast that followed was carried out by all four authors over a number of years. Fieldwork by C.R.C.P. was supported by Liverpool University, Department of Geology. Initial fieldwork by A.B.S. was undertaken with the aid of NERC postdoctoral grant no. GRG/140 and follow-up work was carried out at the British Museum (Natural History). S.K.D. undertook some fieldwork, first during tenure of a NERC Research studentship at Liverpool University, and later a Royal Society European Science Exchange Programme Fellowship at Trinity College, Dublin.

Considerable help and encouragement was received from Mr C. W. Wright, particularly in unravelling the systematics of the various holasteroid echinoids, and he was kind enough to give access to his large collection of echinoderms from Wilmington and elsewhere. Dr C. J. Wood of the British Geological Survey made the collections in the Geological Museum available for study, for which we are grateful. We would also like to thank Mr D. N. Lewis, British Museum (Natural History), for assistance in tracing some of the more obscure crinoid references. Dr R. P. S. Jefferies and Mr C. W. Wright were kind enough to read through much of this paper and made many useful suggestions.

Scanning electron micrographs on Pls 44–49 were taken by Mr C. J. Veltcamp; those on Pls 50–52 were printed by Mr D. J. McCabe. The photography for Pls 1–40 was done by the Photographic Studio, British Museum (Natural History).

References

Agassiz, L. 1836. Prodrome d'une Monographie des Radiaires ou Échinodermes. *Mèm. Soc. neuchâtel. Sci. nat.*, **1:** 168–199.

—— 1838. Des Salenies. *Monographies d'Échinodermes vivans et fossiles*, **1.** 32 pp., 5 pls. Neuchâtel. See Desor 1842.

—— 1839–40. Description des Échinodermes fossiles de la Suisse. 1. Spatangoides et Clypéasteroides. *Neue Denkschr. Allg. schweiz. Ges. ges. Naturw.*, Neuchâtel, **3** (3). viii + 101 pp., 14 pls (1–13bis). (1839). 2. Cidarides. *Loc. cit.* **4** (2). iv + 108 pp., 11 pls (14–23, 21a). (1840*a*).

—— 1840*b*. *Catalogus systematicus ectyporum echinodermatum fossilium musei Neocomensis.* 20 pp. Petitpierre, Neuchâtel.

—— 1863. List of echinoderms sent to different institutions in exchange for other specimens. *Bull. Mus. comp. Zool. Harv.*, Cambridge, Mass., **1:** 17–28.

—— **& Desor, E.** 1846–47. *Catalogue raisonnè des familles, des genres et des èspèces de la classe des èchinodermes.* 167 pp. Paris. (*Annls Sci. nat.*, Paris, **6:** 305–347; **7:** 129–168; **8:** 5–35 & 355–380).

Barel, C. D. N. & Kramers, P. G. N. 1977. A survey of the echinoderm associates of the north-east Atlantic area. *Zool. Verh. Leiden*, **156:** 1–159.

Blake, D. B. 1973. Ossicle morphology of some Recent asteroids and description of some west American fossil asteroids. *Univ. Calif. Publs geol. Sci.*, Berkeley, **104.** 59 pp.

Blank, R. G. & Ellis, C. H. 1982. The probable range concept applied to the biostratigraphy of marine microfossils. *J. Geol.*, Chicago, **90:** 415–433.

Breimer, A. 1978. General morphology—Recent crinoids. *In* Moore, R. C. & Teichert, C. (eds), *Treatise on Invertebrate Paleontology*, **T** (Echinodermata 2): T9–T58. Lawrence.

Breton, G. 1979. Les astéries du Crétacé de Normandie. *Bull. trim. Soc. gèol. Normandie Amis Mus. Havre*, **65** (4): 5–87, 8 pls.

—— 1984. *Comptoniaster* gen. nov. de Goniasteridae du Mesozoïques. *Symbioses*, Olivet, **15:** 244–245.

Brongniart, B. G. 1822. Sur quelque terrains de Craie hors du Basin de Paris. *In* Cuvier, G., *Recherches sur les Ossemens fossiles* **2** (2): 316–337. Paris.

Bronn, H. G. 1834–37. *Lethaia Geognostica*, **I.** 544 pp. Stuttgart.

—— 1860. Amphorozoen. *Klassen und Ordnungen des Thier-Reichs*, **I.** 434 pp. Leipzig & Heidelberg.

Bucaille, E. 1872. Échinides fossiles du Département de la Seine-Inférieure. *Bull. Soc. gèol. Normandie*, Le Havre, **1:** 1–136.

—— 1883. Études sur les Échinides de la Seine Inférieure. *Bull. Soc. gèol. Normandie*, Le Havre, **8:** 16–39.

Carpenter, P. H. 1880*a*. On some undescribed Comatulae from the British Secondary rocks. *Q. Jl geol. Soc. Lond.*, **36:** 36–55.

—— 1880*b*. On some new Cretaceous Comatulae. *Q. Jl geol. Soc. Lond.*, **36:** 549–558.

Carter, D. J. & Hart, M. B. 1977. Aspects of Mid-Cretaceous stratigraphical micropalaeontology. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **29** (1): 1–135.

Casey, R. 1960. A new echinoid from the Lower Cretaceous (Albian) of Kent. *Palaeontology*, London, **3:** 260–264.

—— 1961. The stratigraphical palaeontology of the Lower Greensand. *Palaeontology*, London, **3:** 487–621, pls 77–84.

Cayeux, L. 1961. Repartition des échinides des étages Albien, Vraconien, des zones remaniées du Cenomanien inférieur du Bec de Caux. *Bull. Soc. géol. Normandie*, Le Havre, **51:** 1–12.

—— 1963. Repartition des échinides reguliers du Cenomanien du Pays de Caux. *Bull: Soc. géol. Normandie*, Le Havre, **53:** 13–25.

—— **& Villoutreys, O. de** 1965. Repartition des échinides irreguliers (1e partie). Holectypoida et Cassiduloida du Cenomanien du Bec de Caux. *Bull. Soc. géol. Normandie*, Le Havre, **54:** 35–47.

Clark, A. H. 1908. New genera of unstalked crinoids. *Proc. biol. Soc. Wash.*, **21:** 125–136.

Clark, H. L. 1917. Hawaiian and other Pacific Echini. *Mem. Mus. comp. Zool. Harv.*, Cambridge, Mass., **46:** 85–283.

Claus, C. F. W. 1876–80. *Grundzüge der Zoologie.* 3rd edn. 1254 pp. (1876). 4th edn, **2.** 522 pp. (1880). Marburg & Leipzig.

Cotteau, G. H. 1862–67. *Paléontologie Française.... Terrain Crétacé* **7** (Échinides). 892 pp., Atlas pls 1007–1204. Paris.

—— 1865–76. Études sur les Échinides fossiles du Département de l'Yonne. Terrain Crétacé (suite). Étage Cénomanien. *Bull. Soc. Sci. hist. nat. Yonne*, Auxerre, **19:** 195–263, 4 pls. (1865). Étage Turonien. *Loc. cit.*, **30:** 47–103, 6 pls. (1876).

—— **& Triger, J.** 1857–69. *Échinides du departement de la Sarthe consideres au point de vue zoölogique et stratigraphique.* 455 pp. 65 pls. Paris.

d'Archiac, E. 1847. Rapport sur les fossiles du tourtia, légués par M. Léveillé à la Société Géologique de France. *Mém. Soc. géol. Fr.*, Paris, (2) **2** (2): 291–351, pls 13–25.

—— **& Haime, J.** 1853. *Description des animaux fossiles du groupe nummulitique de l'Inde.* 373 pp., 36 pls. Paris.

Delage, Y. & Hérouard, E. 1903. Les échinodermes. *Traité de Zoologie concrète*, **3.** 495 pp. Paris.

Desmarest, A. 1825. Oursin. *In* Levrault, F. G. (ed.), *Dictionnaire des Sciences Naturelles*, **37:** 59–104. Strasbourg.

Desor, E. 1842. Der Galérites. *Monographies d'Échinodermes vivans et fossiles*, **3.** 94 pp., 13 pls. Neuchâtel. See Agassiz 1838.

—— 1855–58. *Synopsis des Échinides fossiles.* 490 pp., 44 pls. Paris.

Dixon, F. 1850. *The geology and fossils of the Tertiary and Cretaceous formations of Sussex.* 422 pp. London.

—— **& Jones, T. R.** 1878. *The geology of Sussex; or the geology and fossils of the Tertiary and Cretaceous formations of Sussex.* 469 pp., 64 pls. Brighton.

Donovan, S. K. 1984. Stem morphology of the Recent crinoid *Chladocrinus* (*Neocrinus*) *decorus*. *Palaeontology*, London, **27:** 825–841.

d'Orbigny, A. 1850. *Prodrome de Paléontologie stratigraphique universelle des animaux mollusques et rayonnés*, **2.** 427 pp. Paris.

—— 1854–56. Échinoides irreguliers. *Paléontologie Française*, **IV.** 596 pp., pls 801–1006. Paris.

Drummond, P. V. O. 1970. The Mid-Dorset swell. Evidence of Albian–Cenomanian Movements in Wessex. *Proc. Geol. Ass.*, London, **81:** 679–714.

Duncan, P. M. 1889. A revision of the genera and great groups of the Echinoidea. *J. Linn. Soc.*, London, (Zool.) **23:** 1–311.

Durham, J. W. & Melville, R. V. 1957. A classification of echinoids. *J. Paleont.*, Menasha, **31:** 242–272.

Ernst, G. 1972. Grundfragen der Stammesgeschichte bei irregulären Echiniden der nordwesteuropäischen Oberkreide. *Geol. Jb.*, Hannover, (A) **4:** 63–175, 7 pls.

Fell, H. B. & Pawson, D. L. 1966. Echinacea. *In* Moore, R. C. (ed.), *Treatise on Invertebrate Paleontology*, U (Echinodermata 3): U367–U440. Lawrence.

Fischer, A. G. 1966. Spatangoids. *In* Moore, R. C. (ed.), *Treatise on Invertebrate Paleontology*, **U** (Echinodermata 3): U543–U640. Lawrence.

Fitton, W. H. 1836. Observations on the strata between the Chalk and the Oxford Oolite in South East England. *Trans. geol. Soc. Lond.*, **4:** 103–324.

Folk, R. L. 1968. *Petrology of sedimentary rocks.* 170 pp. Austin, Texas.

Forbes, E. 1841. *A history of British starfishes and other animals of the class Echinodermata.* 267 pp. London.

—— 1848. On the Asteriadae found fossil in British Strata. *Mem. geol. Surv. U.K.*, London, **2** (2): 457–482.

—— 1849–56. Figures and descriptions illustrative of British organic remains. Dec. **1,** 10 pls (1849). Dec. 3, 10 pls (1850*b*). Dec. **4,** 10 pls (1852). Dec. **5,** 10 pls (1856). *Mem. geol. Surv. U.K.*, London.

—— 1850*a*. On *Cardiaster*, a new genus of Cretaceous Echinidae allied to *Holaster*. *Ann. Mag. nat. Hist.*, London, **6** (2): 442–444.

Frič, A. 1911. Studien im Gebiete der Böhmischen Kreideformation. Erganzung zu Band I. *Arch. naturw. LandsDurchforsch. Böhmen*, Prague, **15** (1): 1–101.

Gale, A. S. 1987. Goniasteridae (Asteroidea, Echinodermata) from the Late Cretaceous of north-west Europe. 1. Introduction. The genera *Metopaster* and *Recurvaster*. *Mesozoic Res.*, Leiden, **1** (1): 1–69.

Geinitz, F. E. 1871–75. Das Elbthalgebirge in Sächsen. *Palaeontographica*, Stuttgart, **20:** 63–93.

Ghiold, J. 1982. Observations on the clypeasteroid *Echinocyamus pusillus* (O. F. Müller). *J. exp. mar. Biol. Ecol.*, Amsterdam, **61:** 57–74.

Girod, J.-P. 1964. Sur trois comatules du Vercours. *Trav. Lab. Géol. Univ. Grenoble*, **40:** 127–130.

Gislén, T. 1924. Echinoderm studies. *Zool. Bidr. Upps.*, **9:** 1–330.

—— 1925. Some Mesozoic comatulids. *Ann. Mag. nat. Hist.*, London, (9) **16:** 1–30.

Goldfuss, A. 1829–31. Divisio secunda: Radiariorum reliquae. *Petrefacta Germaniae*, **I:** 115–221, pls 39–45. Dusseldorf.

Gras, C. J. A. 1849. Description des oursins fossiles du département de l'Isère. *Bull. Soc. Statist. Sci. nat. Arts ind. Dép. Isère*, Grenoble, (1) **4:** 293–381.

Gray, J. E. 1825. An attempt to divide the Echinida, or sea eggs, into natural families. *Ann. Phil.*, London, **10:** 423–431.

—— 1835. On the genera distinguishable in *Echinus*. *Proc. zool. Soc. Lond.*, **3:** 57–60.

—— 1840. A synopsis of the genera and species of the class Hypostoma (*Asterias* Linn.). *Ann. Mag. nat. Hist.*, London, (1) **6:** 175–184, 275–290.

—— 1847. Descriptions of some new genera and species of Asteriadae. *Proc. zool. Soc. Lond.*, **1847:** 72–83.

Hancock, J. M. 1969. Transgression of the Cretaceous sea in south-west England. *Proc. Ussher Soc.*, Camborne, **2:** 61–83.

Harper, C. 1981. Inferring succession of fossils in time: the need for a quantitative approach. *J. Paleont.*, Tulsa, **55:** 442–452.

Hart, M. B. 1983. Planktonic foraminifera from the Cenomanian of the Wilmington quarries (SE Devon). *Proc. Ussher Soc.*, Camborne, **5:** 406–410.

Hay, W. W. 1972. Probabilistic stratigraphy. *Eclog. geol. Helv.*, Basel, **65:** 255–266.

—— 1974. Implications of probabilistic stratigraphy for chronostratigraphy. *Verh. naturf. Ges. Basel*, **86:** 164–171.

Hess, H. 1955. Die fossilen Astropectiniden (Asteroidea). Neue Beobachtungen und Übersicht über die bekannten Arten. *Schweiz. palaeont. Abh.*, Basel, **71** (3). 113 pp., 4 pls.

—— 1970. Schlangensterne und Seesterne aus dem oberen Hauterivien 'Pierre Jaune' von St Blaise bei Neuchâtel. *Eclog. geol. Helv.*, Basel, **63:** 1069–1091.

Holmes, S. C. A. 1935. The periproctal plates of *Discoidea*. *Geol. Mag.*, London, **72:** 470–478.

Hughes, R. N. & Hughes, H. P. I. 1971. A study of the gastropod *Cassis tuberosa* (L.) preying upon sea urchins. *J. exp. mar. Biol. Ecol.*, Amsterdam, **7:** 305–314.

Huxley, T. H. & Etheridge, R. 1865. *A catalogue of the collection of fossils in the Museum of Practical Geology*. 381 pp. London.

Ikeda, H. 1936. Preliminary note on a new Family of the Cidaroidea. *Annotnes zool. jap.*, Tokyo, **15:** 486–489.

Jackson, R. T. 1912. Phylogeny of the Echini with a revision of Paleozoic species. *Mem. Boston Soc. nat. Hist.*, **7:** 1–490.

Jarvis, I. & Woodroof, P. B. 1984. Stratigraphy of the Cenomanian and basal Turonian (Upper Cretaceous) between Branscombe and Seaton, SE Devon, England. *Proc. Geol. Ass.*, London, **95:** 193–216.

Jensen, M. 1981. Morphology and classification of Euechinoidea Bronn, 1860. A cladistic analysis. *Vidensk. Meddr dansk naturh. Foren.*, Copenhagen, **143:** 7–99.

Jukes-Browne, A. J. 1898. On an outlier of Cenomanian and Turonian near Honiton. *Q. Jl geol. Soc. Lond.*, **54:** 239–250.

—— **& Hill, W.** 1900–04. The Cretaceous rocks of Britain. **1,** Gault and Upper Greensand of England. v + 499 pp., 5 pls (1900). **2,** Lower and Middle Chalk of England. xiii + 568 pp., 8 pls (1903). **3,** The Upper Chalk of England. x + 566 pp., 9 pls (1904). *Mem. geol. Surv. U.K.*, London.

Kennedy, W. J. 1970. A correlation of the Uppermost Albian and the Cenomanian of South-West England. *Proc. Geol. Ass.*, London, **81:** 613–677.

Kier, P. M. 1962. Revision of the cassiduloid echinoids. *Smithson. misc. Collns*, Washington, **144** (3). 262 pp.

—— 1967. Sexual dimorphism in an Eocene echinoid. *J. Paleont.*, Tulsa, **41:** 988–993.

—— 1977. The poor fossil record of the regular echinoid. *Paleobiol.*, Menlo Park, **3:** 168–174.

—— 1981. A bored Cretaceous echinoid. *J. Paleont.*, Tulsa, **55:** 656–659.

Klein, J. T. 1734. *Naturalis dispositio Echinodermatum* . . .79 pp., 36 pls. Gdani.

König, C. 1825. *Icones fossilium sectiles.* 2nd edn, **1.** 4 pp., 8 pls. London.

Lamarck, J. B. P. 1816. *Histoire naturelle des animauux sans vertebres*, **3.** 770 pp. Paris.

Lambert, J. 1882. Note sur l'étage Turonien du département de l'Yonne. *Bull. Soc. Sci. hist. nat. Yonne*, Auxerre, **35:** 144–173.

—— 1888. Échinides. Description de quelques éspèces de la Craie de l'Yonne. *Bull. Soc. Sci. hist. nat. Yonne*, Auxerre, **41:** 400–419.

—— 1894. Étude comparative sur la repartition des échinides Crétacé dans l'Yonne et dans l'est du Bassin de Paris. *Bull. Soc. Sci. hist. nat. Yonne*, Auxerre, **48:** 3–87.

—— 1895. Essai d'une monographie du genre *Micraster* et notes sur quelques échinides. *In* Grossouvre, A. de, Recherches sur la Craie Supérieure **1** (1): 149–267. *Mém. Serv. Carte géol. dét. Fr.*, Paris.

—— 1900. Étude sur quelques Échinides de l'Infra-lias et du Lias. *Bull. Soc. Sci. hist. nat. Yonne*, Auxerre, **53:** 3–57.

—— 1903. Sur quelques petits *Hemiaster* de la Craie Blanche. *Bull. Soc. Sci. hist. nat Yonne*, Auxerre, **57:** 5–15.

—— 1910. Observations à l'occasion de l'étude de quelques échinides de l'Ardèche et du Garde. *Annls Soc. linn. Lyon*, **56:** 93–98.

—— 1911. Description des Échinides crétacés de la Belgique. Échinides de l'étage Senonien. *Mém. Mus. r. Hist. nat. Belg.*, Brussels, **4:** 1–78.

—— 1914. [Review of] The evolution of the cretaceous Asteroidea, by W. R. Spencer. *Revue crit. Paléozool.*, Paris, **18:** 27–28.

—— 1917. Note sur quelques Holasteridae. *Bull. Soc. Sci. hist. nat. Yonne*, Auxerre, **63:** 191–223.

—— 1920. Sur quelques genres nouveaux d'Échinides. *Mém. Soc. acad. Agric. Sci. Dép. Aube*, Troyes, (3) **56:** 145–174.

—— **& Thiéry, P.** 1909–25. *Essai de nomenclature raisonnée des échinides.* 607 pp., 15 pls. Paris.

Latreille, P. A. 1825. *Familles naturelles du règne animal.* 570 pp. Paris.

Lawrence, J. M. 1975. On the relationship between marine plants and sea urchins. *Oceanography mar. Biol.*, London, **13:** 213–286.

Leske, N. G. 1778. *Jacobi Theodori Klein Naturalis dispositio Echinodermatum. Additamenta ad I. T. Klein naturalem dispositionem Echinodermatum* . . . 175 pp. Paris.

Lewis, D. N. 1986. The Cretaceous echinoid genus *Boletechinus*, with notes on the phylogeny of the Glyphocyphidae and Temnopleuridae. *Bull. Br. Mus. nat. Hist.*, London, (Geol.) **40** (2): 59–90.

Loriol, P. de 1869. *In* Loriol, P. de & Gillieron, V. (q.v.).

—— 1873. *Échinologie Helvetique. Terrain Crétacé, Description des Échinides des terrains Crétacés de la Suisse.* 398 pp., 33 pls. Geneva.

—— 1874. Description de quelques astérides du terrain Néocomien des environs de Neuchâtel. *Mém. Soc. Sci. nat. neuchâtel*, **4** (2, part 2): 3–19, 2 pls.

—— 1884. Notes pour servir à l'étude des Échinodermes. *Recl. zool. suisse*, Geneva, **1:** 605–643, pls 31–35.

—— 1887. Recueil d'études paléontologiques sur la Faune Crétacique du Portugal. **II.** Description des Echinodermes (1, Échinides réguliers ou endocycles). 68 pp., 10 pls. *Mém. Commun géol. Port.*, Lisbon.

—— 1894. Notes pour servir a l'étude des Echinodermes. *Revue suisse Zool.*, Geneva, **2:** 467–497.

—— **& Gillieron, V.** 1869. Monographie paléontologique et stratigraphique du l'étage Urgonien inferieur du Landeron (Cant. de Neuchâtel). *Neue Denkschr. Alleg. schweiz. Ges. ges. Naturw.*, Zürich, **23** (55): 4–94.

MacFadyen, W. A. 1970. *Geological highlights of the west country.* 296 pp. London.

M'Coy, F. 1848. On some new Mesozoic Radiata. *Ann. Mag. nat. Hist.*, London, **2** (2): 397–428.

Mantell, G. A. 1822. *The fossils of the South Downs, or an illustration of the geology of Sussex.* 327 pp. London.

Matthews, S. C. 1973. Notes on open nomenclature and on synonymy lists. *Palaeontology*, London, **16** (4): 713–719.

Mercier, J. 1935. Les Stellérides Mésozoïques du Bassin de Paris (Bordure occidentale). *Mém. Soc. linn. Normandie*, Caen, (n.s., Geol.) **1** (2). 64 pp., 3 pls.

Mauzey, K. P., Birkeland, C. & Dayton, P. K. 1968. Feeding behaviour of asteroids and escape response of their prey in the Puget Sound region. *Ecology, Brooklyn*, **49:** 603–619.

Miller, J. S. 1821. *A natural history of the Crinoidea or lily shaped animals, with observations on the genera Asterias, Eurale, Comatula and Marsupites.* 150 pp. Bristol.

Moore, R. C., Jeffords, R. M. & Miller, T. H. 1968. Morphological features of crinoid columns. *Paleont. Contr. Univ. Kans.*, Lawrence, **45** (Echinodermata **8**). 30 pp., 4 pls.

Morris, J. 1843–54. *A catalogue of British fossils.* 1st edn, 222 pp. (1843). 2nd edn, 372 pp. (1854). London.

Mortensen, T. 1918. The Crinoidea of the Swedish Antarctic expedition. *Wiss. Ergebn. schwed. Südpolarexped.*, Stockholm, **4:** 1–23.

—— 1928–52. *A Monograph of the Echinoidea.* **1,** Cidaroidea. 551 pp., 88 pls (1928). **2,** Bothriocidaroida, Melonechinoida, Lepidocentroida and Stirodonta. 647 pp., 89 pls (1935). **3** (1), Aulodonta, with additions to volume 2. 369 pp., 79 pls (1940). **3** (2 + 3), Camarodonta. 553 + 466 pp., 56 + 66 pls (1943). **4** (1 + 2), Holectypoida, Cassiduloida + Clypeasteroida. 363 + 471 pp., 14 + 72 pls (1948). **5** (1 + 2), Spatangoida. 432 + 593 pp., 25 + 64 pls (1950–51). Copenhagen.

—— 1939. New Echinoidea (Aulodonta) (preliminary notice). *Vidensk. Meddr dansk naturh. Foren.*, Copenhagen, **103:** 547–550.

Müller, A. H. 1953. Die isolierten Skelettelemente der Asteroidea (Asterozoa) aus der Obersenonen Schreibkreide von Rügen. *Beih. Z. Geol.*, Berlin, **8:** 1–66.

Parkinson, J. 1811. *Organic remains of a former world,* **3.** 479 pp. London.

Paul, C. R. C. 1982. The adequacy of the fossil record. *In* Joysey, K. A. & Friday, A. E. (eds), *Problems of phylogenetic reconstruction*: 75–117. London (Systematics Association).

—— 1985. The adequacy of the fossil record reconsidered. *In* Cope, J. C. W. & Skelton, P. W. (eds), Evolutionary case histories from the fossil record. *Spec. Pap. Palaeont.*, London, **33:** 7–15.

Perrier, J. O. E. 1884. Mémoire sur les étoiles de mer receuilliés dans la mer d'Antilles et le Golf du Mexique. *Nouv. Archs Mus. Hist. nat. Paris,* (2) **6:** 127–276.

Philip, G. M. & Foster, R. J. 1971. Marsupiate Tertiary echinoids from south-eastern Australia and their zoogeographic significance. *Palaeontology*, London, **14:** 666–695.

Pictet, F. J. 1857. *Traité elementaire de Paléontologie.* (2nd edn), **4.** 768 pp. Paris.

Pisera, A. 1983. Comatulid and roveacrinid crinoids from the Cretaceous of Central Poland. *Palaeont. pol.*, Warsaw, **28:** 385–391.

Pomel, M. A. 1869. *Revue des Échinodermes et leur classification pour servir d'introduction à l'étude des fossiles.* 67 pp. Paris.

—— 1883. *Classification méthodique et Genera des Échinides vivants et fossiles.* Thésès presentés à la faculté des Sciences de Paris. 131 pp. Paris.

Quenstedt, F. A. 1872–74. *Petrefactenkunde Deutschlands.* **III,** Echinodermen (Echiniden). 720 pp. Leipzig.

Rasmussen, H. W. 1950. Cretaceous Asteroidea and Ophiuroidea with special reference to the species found in Denmark. *Danm. geol. Unders.*, Copenhagen, (2) **77.** 134 pp.

—— 1961. A Monograph on the Cretaceous Crinoidea. *Biol. Skr.*, Copenhagen, **12.** 428 pp., 60 pls.

—— 1971. Cretaceous Crinoidea (Comatulida and Roveacrinida) from England and France. *Bull. geol. Soc. Denm.*, Copenhagen, **20:** 285–294.

—— **& Sieverts-Doreck, H.** 1978. *In* Rasmussen, H. W., Articulata. *In* Moore, R. C. & Teichert, C. (eds), *Treatise on Invertebrate Paleontology* **T** (Echinodermata 3): T814–T927. Lawrence, Kansas.

Renevier, P. 1868. Notices géologiques et paléontologiques sur les Alpes Vaudoises et les region environnantes. V, complément de la fauna de Cheville. *Bull. Soc. vaud. Sci. nat.*, Lausanne, **9:** 389–480.

Roman, J. 1983. Échinides 'Marsupiaux' (Fam. Temnopleuridae) dans le Neogène de l'ouest Européen. *Annls Paléont.*, Paris, **69:** 13–43.

Rose, E. P. F. 1978. Some observations on the Recent holectypoid echinoid *Echinoneus cyclostomus* and their palaeoecological significance. *Thalassia jugosl.*, Zagreb, **12:** 299–306.

Savin, L. 1905. Revision des Échinides fossiles du département de l'Isère. *Bull. Soc. Statist. Sci. nat. Arts ind. Dép. Isère,* Grenoble, (4) **8:** 109–315.

Schlüter, C. 1878. Über einige astylide Crinoideen. *Z. dt. geol. Ges.*, Berlin, **30:** 28–66.

—— 1883–92. Die Regularen Echiniden der norddeutschen Kreide. I, Glyphostoma. *Abh. geol. SpecKarte preuss. thür. St.*, Berlin, **4:** 1–72 (1883). II, Cidaridae, Salenidae. *Loc. cit.* **5:** 1–243 (1892).

Schöndorf, F. 1906. Die Organisation und systematische Stellung der Sphaeriten. *Arch. Biontol.*, Berlin, **1:** 245–306.

Schulz, M. G. & Weitschat, W. 1971. Asteroideen aus der Schreibkreide von Lagerdorf (Holstein) und Hemmoor (Nord Niedersächen). *Mitt. geol.-paläont. Inst. Univ. Hamburg*, **40:** 107–130.

Shaw, A. B. 1964. *Time in stratigraphy.* 365 pp. New York.

—— 1971. The butterfingered handmaiden. *J. Paleont.*, Tulsa, **45:** 1–5.

Sieverts-Doreck, H. 1952. Classification [of crinoids]. *In* Moore, R. C., Lalicker, C. G. & Fischer, A. G., *Invertebrate Fossils*: 613–614. New York.

—— 1958. Über einige Comatulida aus Jura und Kreide. *Neues Jb. Geol. Paläont. Abh.*, Stuttgart, **106:** 245–260.

Sladen, W. P. 1891–93. A Monograph on the British fossil Echinodermata from the Cretaceous Formations. **2,** Asteroidea and Ophiuroidea. (1): 1–28 (1891). (2): 29–66 (1893). *Palaeontogr. Soc.* (*Monogr.*), London. See Spencer, W. K.

Smiser, J. S. 1935. A monograph of the Belgian Cretaceous Echinoids. *Mém. Mus. r. Hist. nat. Belg.*, Brussels, **68:** 1–93.

Smith, A. B. 1978. A functional classification of the coronal pores of regular echinoids. *Palaeontology*, London, **21:** 759–790.

—— 1981. Implications of lantern morphology for the phylogeny of post-Palaeozoic echinoids. *Palaeontology*, London, **24:** 779–801.

—— 1984. *Echinoid palaeobiology*. 190 pp. London.

—— **& Paul, C. R. C.** 1985. Variation in the irregular echinoid *Discoides* during the early Cenomanian. *In* Cope, J. C. W. & Skelton, P. W. (eds), Evolutionary case histories from the fossil record. *Spec. Pap. Palaeont.*, London, **33:** 29–37.

—— **& Wright, C. W.** 1988. Part 1, Cidaroida. *In* British Cretaceous Echinoids. *Palaeontogr. Soc.* (*Monogr.*), London, **142** [In press].

Smith, W. E. 1957*a*. The Cenomanian Limestone of the Beer district, South Devon. *Proc. Geol. Ass.*, London, **68:** 115–133.

—— 1957*b*. Summer field meeting in South Devon and Dorset. *Proc. Geol. Ass.*, London, **68:** 136–152.

—— 1961. The Cenomanian deposits of south-east Devonshire. *Proc. Geol. Ass.*, London, **72:** 91–133.

—— **& Drummond, P. V. O.** 1962. Easter field meeting: the Upper Albian and Cenomanian deposits of Wessex. *Proc. Geol. Ass.*, London, **73:** 335–352.

Sohl, N. F. 1969. The fossil record of shell boring by snails. *Am. Zool.*, Utica, **9:** 725–734.

Sorignet, M. 1850. *Oursins fossiles de deux arrondissements du département de l'Eure*. 83 pp. Paris.

Spencer, W. K. 1905–07. A Monograph on the British fossil Echinodermata from the Cretaceous Formations. **2,** Asteroidea and Ophiuroidea. (3): 67–90 (1905). (4): 91–132 (1907). *Palaeontogr. Soc.* (*Monogr.*), London. See Sladen, W. P.

—— 1913. The evolution of the Cretaceous Asteroidea. *Phil. Trans. R. Soc.*, London, (B) **214:** 99–177.

—— **& Wright, C. W.** 1966. Asterozoans. *In* Moore, R. C. (ed.), *Treatise on Invertebrate Paleontology* **U** (Echinodermata 3): U4–U107. Lawrence, Kansas.

Stokes, R. B. 1977. The echinoids *Micraster* and *Epiaster* from the Turonian and Senonian chalk of England. *Palaeontology*, London, **20:** 805–821.

Sweet, W. C. 1984. Graphic correlation of upper Middle and Upper Ordovician rocks, North American Mid-Continent Province, U.S.A. *In* Bruton, D. L. (ed.), *Aspects of the Ordovician System*: 23–35. Oslo.

Szörényi, E. 1955. Bakonyi Kréta Echinoideák. *Geologica hung.*, Budapest, (Palaeont.) **26:** 1–286, pls 1–22.

Taylor, J. D., Cleevely, R. J. & Morris, N. J. 1983. Predatory gastropods and their activities in the Blackdown Greensand (Albian) of England. *Palaeontology*, London, **26:** 521–554.

Ubaghs, G. 1978. Skeletal morphology of fossil crinoids. *In* Moore, R. C. & Teichert, C. (eds), *Treatise on Invertebrate Paleontology* **T** (Echinodermata 2): T58–T216. Lawrence, Kansas.

Valette, A. 1908. Revision des Echinides fossiles de l'Yonne. *Bull. Soc. Sci. hist. nat. Yonne*, Auxerre, **61:** 185–385.

—— 1917. Note sur les crinoïdes de la Craie Blanche. *Bull. Soc. Sci. hist. nat. Yonne*, Auxerre, **70:** 79–178.

—— 1925. Note sur les débris de Stellerides fossiles du sud-ouest de la France. *Act. Soc. linn. Bordeaux*, **76:** 167–205.

Wagner, C. D. & Durham, J. W. 1966. Holectypoids. *In* Moore, R. C. (ed.), *Treatise on Invertebrate Paleontology* **U** (Echinodermata 3): U440–U450. Lawrence, Kansas.

Webster, G. D. 1974. Crinoid pluricolumnal noditaxis patterns. *J. Paleont.*, Tulsa, **48:** 1283–1288.

Woodward, S. P. 1856. Decade V. [Explanation of] plate II (pp. 1–11). Appendix to Decade V (pp. 1–7). *In* Figures and Descriptions illustrative of British organic remains. *Mem. geol. Surv. U.K.*, London.

Wright, C. W. 1967. Notes on Cretaceous Saleniidae. *Proc. Geol. Ass.*, London, **78:** 9–26.

—— **& Kennedy, W. J.** 1981. The Ammonoidea of the Plenus Marls and the Middle Chalk. 148 pp. *Palaeontogr. Soc.* (*Monogr.*), London.

—— —— 1984. The Ammonoidea of the Lower Chalk. Part 1. 126 pp. *Palaeontogr. Soc.* (*Monogr.*), London.

—— **& Wright, E. V.** 1940. Notes on Cretaceous Asteroidea. *Q. Jl geol. Soc. Lond.*, **46:** 231–248.

Wright, T. 1864–82. Monograph on the British fossil Echinodermata from the Cretaceous formations. **1,** Echinoidea. 371 pp. *Palaeontogr. Soc.* (*Monogr.*), London.

Zittel, K. A. von 1879. *Handbuch der Palaeontologie*, **1.** 765 pp. Munich & Leipzig.

Systematic Index

Acroechinoidea 44
aequimarginatus, Glenotremites 224, 226, 230; pl. 49; pl. 50, figs 1–3, 5; pl. 51, figs 1–5, 8, 9
Allomma 20–1, 29, 74
  normaniae 78
  rhodani 15, 17, 20, 25, 74–8; pl. 10, figs 1–4
altus, Holaster 146, 150–1
angustatus, Pycinaster 195
Apatopygus 23
Antedon incurva 227
  rotunda 227
apiculatus, Goniophorus 55
Aporometra 224
Arbacia conica 93
  granulosa 93
  radiatus 78
argus, Valettaster 195
Articulata 213
Aspidaster 193
  bulbiferus 193
  delgadoi 193
  sp. 193
Asterias quinqueloba 203
Astropectinidae 207
Aurelianaster 194

Balanocidaris velifera 41
benettiae, Cottaldia 15–17, 25, 28, 35, 53, 88–93, 95–6; pl. 13, figs 1–3; pl. 14, fig. 4
benettiae, Diadema 60, 68–9
benettiae, Pseudodiadema 60, 64
bischoffi, Holaster 12–13, 15, 17, 25, 28–30, 35, 146–51, 155; pl. 30, figs 1–4
Bolbaster 178, 181
bonei, Polydiadema 15, 17, 20, 25, 28, 31, 64–9; pl. 8, figs 1–4; pl. 40, figs 2–3
boysii, Oreaster 193
bufo, Hemiaster (*Hemiaster*) 15, 17, 24–5, 30, 173–8, 181; pl. 36, figs 1–4
bulbiferus, Aspidaster 193

Caletaster 202
  girardi 202–3
  sp. 202–3; pl. 43, fig. 6
Calliderma 191, 199, 205
  emma 199
  mosaica 200
  smithiae 199–200
Calycina 44
Camarodonta 78
Camerogalerus cylindricus 106
Caratomus faba 115
  orbicularis 120, 125
  rostratus 119, 125
  trigonopygus 115
Cardiaster 166
  cretaceus 167
  pygmaeus 166–7
  truncatus 16–17, 23–5, 166–7; pl. 19, figs 5–7
Cardiotaxis 167
  cf. *cretacea* 15, 17, 23–5, 167–70; pl. 35, figs 2–4
carentonensis, Glenotremites 224
carinatus, Catopygus 33, 125, 132
carinatus, Holaster 134, 142, 158, 161
carinatus, Nucleolites 125, 132
Cassidulidae 132
Cassiduloida 125
Cassidulus 23
castanea, Conulus 15, 17, 25, 27, 29–30, 35, 106–12; pl. 17, figs 1–3; pl. 18, figs 1–3
Catopygus 22–3, 27–8, 30, 125
  carinatus 33, 125, 132
  columbarius 15, 17, 25, 27, 29–30, 32–5, 125–32; pl. 25, figs 1–4; pl. 26, figs 1–4
  cylindricus 132
cenomanensis, Isocrinus(?) 15, 214–7, 220; pl. 44, figs 1–7
cenomanensis, Labrotaxis 15, 17, 158–61, 165; pl. 33, figs 1–2; pl. 34, figs 1–4
Cidaridae, Cidarinae 37
Cidaris velifera 40–1
  vesiculosa 37, 40
Cidarites ornatus 63
  variolaris 69, 73
Cidaroida, Cidaroidea 37
clathrata, Hyposalenia 15–17, 25, 28, 31, 35, 48–53; pl. 4, figs 1–4
clavigera, Tylocidaris 43
Codiopsis 88
columbarius, Catopygus 15, 17, 25, 27, 29–30, 32–5, 125–32; pl. 25, figs 1–4; pl. 26, figs 1–4
Comatulida 222
comptoni, Comptoniaster 202; pl. 41, fig. 5
Comptoniaster 202
  comptoni 202; pl. 41, fig. 5
conica, Arbacia 93
contexta, Echinopsis 78
Conulidae 106
Conulus 106
  castanea 15, 17, 22, 25, 27, 29–30, 35, 106–12; pl. 17, figs 1–3; pl. 18, figs 1–3
    castanea 30, 108–9, 112; pl. 17, figs 1–3
    rhotomagensis 30, 108–9, 112; pl. 18, figs 1–3
  subrotundus 16–17, 22, 25, 112–5; pl. 19, figs 3–4
coronatus, Stauranderaster 193–4; pl. 41, fig. 2
Cottaldia 21, 33, 88–9
  benettiae 15–17, 25, 28, 35, 53, 88–93, 95–6; pl. 13, figs 1–3; pl. 14, fig. 4
  granulosa 15–17, 25, 28, 35, 53, 89, 91, 93–6; pl. 14, figs 1–3
  rotula 88
  sorigneti 89
Coulonia 207

  neocomiensis 208
  sp. 207–8; pl. 43, fig. 7
crassissimus, *Epiaster* 173
Crateraster 203
  quinqueloba 203
cretacea, *Cardiotaxis* 15, 17, 23–5, 167–70; pl. 35, figs 2–4
Crinoidea 213
Cuneaster hauteriviensis 208
cylindricus, *Camerogalerus* 106
cylindricus, *Catopygus* 132
Cyphosoma difficile 83, 87

delgadoi, *Aspidaster* 193
depressa, *Echinopsis* 78
depressa, *Nucleolites* 106, 112
depressa, *Pyrina* 106
desori, *Diadema* 74, 78
Diadema benettiae 60, 68–9
  bonei 64, 68–9
  desori 74, 78
  lucae 74, 77
  m'coyi 83, 87
  michelini 59, 68–9
  ornatum 59
  pustulata 74, 78
  rhodani 74, 77
  rotulare 83, 87
  subnudum 69
difficilis, *Glyptocyphus* 15, 17, 31, 83–8; pl. 12, figs 1–4
Diplopodia subnuda 69
  variolaris 69
discoidalis, *Glenotremites* 224, 231–3
Discoidea favrina 103
  infera 98
  subuculus 96
Discoides 21–2, 26, 29, 96
  favrinus 15, 17, 21, 25, 100, 103–6; pl. 16, figs 1–3
  inferus 16–17, 21, 25, 98, 101–3; pl. 15, figs 4–6; pl. 19, fig. 2
  subuculus 13, 15, 17, 21, 25, 27, 31, 35, 96–103, 106; pl. 15, figs 1–3; pl. 19, fig. 1
Discoididae 96
distinctus, *Micraster* 14–15, 17, 24–5, 170–3; pl. 38, fig. 3; pl. 39, figs 1–4
dondeyi, *Glenotremites* 224
Dorocidaris essenensis 37
Dumblea 89

Echinacea 44
Echinites pyriformis 125, 132
  subuculus 96
Echinobrissus morrisii 133
  placentula 132
  subquadratus 132–3
Echinoconus castanea 106
  subrotundus 112
Echinocyamus 22
Echinocyphus difficilis 87
  rotatus 83, 88
Echinogalerus 21–2, 27, 29, 115
  faba 15, 17, 21–2, 27, 31, 114–20; pl. 20, figs 1–4; pl. 21, figs 1–4
  rostratus 15, 17, 21–2, 25, 27, 31–3, 35, 119–25; pl. 22, figs 1–4; pl. 23, figs 1–4; pl. 24, figs 6–7
Echinoneus 21–2
Echinopsis contexta 78
  depressa 78
  latipora 78
  pusilla 78, 83
Echinus benettiae 89
  granulosus 89, 93
  petaliferus 44
  radiatus 78, 82
emma, *Calliderma* 199
Epiaster 173
  crassissimus 173
  distinctus 170, 173
  polygonus 173
  trigonalis 173
  tumidus 173
essenensis, *Stereocidaris* 15, 17, 21–2, 25, 27, 31, 37–40; pl. 1, figs 1–3; pl. 2, figs 7–8
essenensis, *Typocidaris* 37
Euechinoidea 44

faba, *Echinogalerus* 15, 17, 21–2, 25, 27, 31, 114–20; pl. 20, figs 1–4; pl. 21, figs 1–4
favosus, *Goniophorus* 55
favrei, *Discoides* 103
favrinus, *Discoides* 15, 17, 21, 25, 100, 103–6; pl. 16, figs 1–3

Galerites castanea 106, 112
  rhotomagensis 106, 112
Galeritidae 115
girardi, *Caletaster* 202–3
Glenotremites 224–7
  aequimarginatus 224, 226, 230; pl. 49; pl. 50, figs 1–3, 5; pl. 51, figs 1–4, 8–9
  carentonensis 224
  discoidalis 224, 231–3
  dondeyi 224
  loveni 224
  paradoxus 224, 231; pl. 50, fig. 7
  rosaceus 231
  rotundus 224, 226–8, 230; pl. 50, fig. 4; pl. 51, fig. 7
  schlueterianus 224
  tourtiae 224
  valettei 224
  sp. 226, 233; pl. 50, fig. 6
Glyphocyphidae 78
Glyphocyphus 21, 78
  difficilis 87
  pulchellus 78

  radiatus 15, 17, 25, 31, 78–83; pl. 11, figs 1–4; pl. 40, fig. 4
Glypticus koninckii 78, 83
Glyptocyphus 21, 83
  difficilis 15, 17, 25, 31, 83–8; pl. 12, figs 1–4
Goniaster angustatus 195
  comptoni 202
Goniasteridae 192, 198
  sp. A 205; pl. 43, figs 1–2
  sp. B 205–7; pl. 43, fig. 5
Goniasterinae 198
Goniophorus 20, 55
  apiculatus 55
  favosus 55
  lunulatus 15, 17, 25, 55–9; pl. 6, figs 1–4
Goniopygus 15
grandis, Phocidaster 195, 197–8; pl. 41, fig. 4
granosus, Isocrinus(?) 220, 222; pl. 47, figs 1, 5; pl. 48, fig. 3
granulosa, Cottaldia 15–17, 25, 28, 35, 53, 89, 91, 93–6; pl. 14, figs 1–3
granulostriata, Prionocidaris 16–17, 25, 43–4; pl. 2, figs 3, 6

hauteriviensis, Cuneaster 208
Helodiadema 88
Hemiaster 31, 173
  (*Bolbaster*) *nasutulus* 16–17, 24–5, 174, 177–82; pl. 37, figs 1–4; pl. 38, figs 1–2
  (*Hemiaster*) *bufo* 15, 17, 24–5, 30, 173–8, 181; pl. 36, figs 1–4
  prunella 181
Hemiasteridae 173
Heteraster 173
Hippasteria spinosa 192
Holaster 28, 134
  altus 146, 150–1
  bischoffi 12–13, 15, 17, 25, 28–30, 35, 146–51, 155; pl. 30, figs 1–4
  carinatus 134, 142, 158, 161
  cretaceus 167
  icaunensis 166
  laevis 15, 17, 23, 25, 33, 134–5, 138, 141–6; pl. 29, figs 1–4
  marginalis 142
  nodulosus 15, 17, 23, 25, 28–30, 33, 35, 134–42, 145–6; pl. 27, figs 1–4; pl. 28, figs 1–6
  revestensis 15, 17, 25, 153, 155–7; pl. 35, fig. 1
  subglobosus 15, 17, 25, 30, 149–55; pl. 31, figs 1–4; pl. 40, fig. 1
  suborbicularis 161, 165–6
  transversus 142
Holasteridae, Holasteroida 134
Holectypoida 96
Holectypus depressus 21
Holocrinidae 213–4
humilis, Pycinaster 197
Hyposalenia 20, 33, 48–55
  clathrata 15–17, 25, 28, 31, 35, 48–53; pl. 4, figs 1–4
  umbrella 15–17, 25, 28, 35, 53–5; pl. 5, figs 1–3

incurva, Antedon 227
inferus, Discoides 16–17, 21, 25, 98, 101–3; pl. 15, figs 4–6; pl. 19, fig. 2
Irregularia 96
Isocrinida 213–4
Isocrinus neuvillensis 214, 216
Isocrinus(?) 214
  cenomanensis 15, 214–7, 220; pl. 44, figs 1–7
  granosus 220
  cf. *granosus* 222; pl. 47, figs 1, 5; pl. 48, fig. 3
  undulatus sp. nov. 15, 216–21; pls 45–6; pl. 47, figs 2, 4; pl. 48, figs 1–2, 4

koninckii, Glypticus 78, 83

Labrotaxis 158
  cenomanensis 15, 17, 25, 158–61, 165; pl. 33, figs 1–2; pl. 34, figs 1–4
  tricarinata 15, 17, 23–5, 30, 161–6; pl. 32, figs 1–4; pl. 33, fig. 3
laevis, Conulus 108
laevis, Holaster 15, 17, 23, 25, 33, 134–5, 138, 141–6; pl. 29, figs 1–4
laevis, Pyrina 106, 112
latipora, Echinopsis 78
Lophidiaster ornatus 208
Loriolometra 224
loveni, Glenotremites 224
lucae, Diadema 74, 77
lunulatus, Goniophorus 15, 17, 25, 55–9; pl. 6, figs 1–4

Magnosia 88
  sequana 89
marginalis, Holaster 142
Mastaster 203
  villersensis 189, 203–4; pl. 42, figs 3–7; pl. 43, fig. 3
    wrighti 205
  sp. 204–5; pl. 43, fig. 4
m'coyi, Diadema 83, 87
Mediaster aequalis 192
Metacrinus 213
Metopaster 189–91, 198
  parkinsoni 199
  polyplacus 199
  thoracifer 189, 198
  sp. A 198–9; pl. 42, fig. 2
  sp. B 199
  sp. C 199
michelini, Micraster 173
michelini, Tiaromma, 15, 17, 20–1, 25, 28, 30, 59–64, 68–9; pl. 7, figs 1–3
Micraster 30, 170

  distinctus 14–15, 17, 24–5, 170–3; pl. 38, fig. 3; pl. 39, figs 1–4
  michelini 173
Micrasteridae 170
Micropedina 88–9
morrisii, Ochetes 133; pl. 24, fig. 5
mosaica, Calliderma 200

nasutulus, Hemiaster (Bolbaster) 15, 17, 24–5, 174, 177–82; pl. 37, figs 1–4; pl. 38, figs 1–2
neocomiensis, Coulonia 208
neuvillensis, Isocrinus(?) 214, 216
nodulosus, Holaster 15, 17, 23, 25, 28–30, 33, 35, 134–42, 145–6; pl. 27, figs 1–4; pl. 28, figs 1–6
normaniae, Allomma 78
Notocrinacea, Notocrinidae 224
Notocrinus 224
Nucleolites castanea 106, 112
  columbaria 125, 132
  depressa 106, 112
  morrisii 133
Nucleolitidae 125
Nucleopygus 133
nucula, Conulus 108

ocellatus, Valettaster 194–5; pl. 41, fig. 1
Ochetes 22–3, 132
  morrisii 133; pl. 24, fig. 5
  cf. *placentula* 15, 17, 25, 132–4; pl. 24, figs 1–4
oligoplax, Pentagonaster 200
Ophryaster 200
  sulcatus 200–2; pl. 42, fig. 1
orbicularis, Caratomus 120, 125
Oreaster boysii 193
  ocellatus 194
ornatus, Cidarites 63
ornatus, Lophidiaster 208
ornatum, Pseudodiadema 60, 64

paradoxus, Glenotremites 224, 231; pl. 50, fig. 7
parkinsoni, Metopaster 199
Paxillosida 207
Peltastes clathratus 48
  umbrella 53
Pentacrinidae 214
Pentacrinus 214
  cenomanensis 214
Pentagonaster oligoplax 200
Peroniaster nasutulus 178
personata, Salenia 44
petalifera, Salenia 17, 25, 44–8; pl. 3, figs 1–4
Phocidaster 195, 197
  grandis 195, 197–8; pl. 41, fig. 4
placentula, Ochetes 15, 17, 25, 132–4; pl. 24, figs 1–4
Polydiadema 20, 29, 64
  bonei 15, 17, 20, 25, 28, 31, 64–9; pl. 8, figs 1–4; pl. 40, figs 2–3
polygonus, Epiaster 173
polyplacus, Metopaster 199
Prionocidaris 43
  granulostriata 16–17, 25, 43–4; pl. 2, figs 3, 6
prunella, Hemiaster (Bolbaster) 181
Pseudodiadema benettiae 60, 64
  michelini 60, 64
  ornatum 60
  pseudoornatum 64, 69
  rhodani 74
  schlueteri 64
  tenue 64, 69
  variolare 69
Pseudodiadematidae 59
pseudoornatum, Pseudodiadema 64, 69
Psychocidaridae 40
pulchellus, Glyphocyphus 78
pusilla, Echinopsis 78, 83
pustulata, Diadema 74, 78
Pycinaster 195, 197–8
  angustatus 195
  humilis 197
  sp. 195–6; pl. 41, fig. 3
Pycinasteridae 195
pygmaeus, Cardiaster 166–7
Pygurus 15
Pyrina depressa 106
  laevis 106, 112

quinqueloba, Crateraster 203

radiatus, Glyphocyphus 15, 17, 25, 31, 78–83; pl. 11, figs 1–4; pl. 40, fig. 4
Remesimetra 224
revestensis, Holaster 15, 17, 20, 25, 153, 155–7; pl. 35, fig. 1
rhodani, Allomma 15, 17, 20, 25, 74–8; pl. 10, figs 1–4
rhotomagensis, Conulus castanea 108–9, 112; pl. 18, figs 1–3
rhotomagensis, Echinoconus 106
rhotomagensis, Galerites 106, 112
roissyi, Tetragramma 73
rosaceus, Glenotremites 231
rostratus, Echinogalerus 15, 17, 21–2, 25, 27, 31–3, 35, 119–25; pl. 22, figs 1–4; pl. 23, figs 1–4; pl. 24, figs 6–7
Rostrogalerus rostratus 120
rotatus, Echinocyphus 83, 88
rotula, Cottaldia 88
rotulare, Diadema 83, 87
rotundus, Glenotremites 224, 226–8, 230; pl. 50, fig. 4; pl. 51, fig. 7

Salenia 20, 44–8
  clathrata 48
  lunulata 55
  personata 44
  petalifera 15, 25, 44–8; pl. 3, figs 1–4
  umbrella 53

Saleniidae 44
schleuterianus, Glenotremites 224
Schlueterometra 224
schluteri, Pseudodiadema 64
Seirocrinus 214
Semiometra 224, 227, 230
sequana, Magnosia 89
smithiae, Calliderma 199–200
sorigneti, Cottaldia 89
Spatangoida 170
Spatangus 23
  bufo 173
  laevis 142
  nodulosus 134
  subglobosus 151
  truncatus 166
Sphaerasteridae 194
Sphaerometra incurva 227
Sphaeronometra aequimarginata 230
Stauranderaster 193
  coronatus 193–4; pl. 41, fig. 2
Stauranderasteridae 193
Stellaster comptoni 202
Stereocidaris 20, 37–41, 43
  uniformis essenensis 15, 17, 20, 25, 28, 37–40; pl. 1, figs 1–3; pl. 2, figs 7–8
Stirodonta 44
subglobosus, Holaster 15, 17, 25, 30, 149–55; pl. 31, figs 1–4; pl. 40, fig. 1
subnudum, Tetragramma variolare 69–74; pl. 9, figs 1–4
suborbicularis, Holaster 161, 165–6
subquadratus, Echinobrissus 132
subrotundus, Conulus 16–17, 22, 25, 112–5; pl. 19, figs 3, 4
subuculus, Discoides 13, 15, 17, 21, 25, 27, 31, 35, 96–103, 106; pl. 15, figs 1–3; pl. 19, fig. 1
sulcatus, Ophrydaster 200–2; pl. 42, fig. 1
sulcatus, Tomidaster 200

Temnopleuroida 83
tenue, Pseudodiadema 64, 69
Tetragramma 20–1, 29, 69
  roissyi 73
  variolare subnudum 15, 17, 20, 25, 28, 69–74; pl. 9, figs 1–4
Tholaster 194
Tholasterina 194
thoracifer, Metopaster 189, 198
Tiaromma 20–1, 27, 29, 59
  michelini 15, 17, 25, 28, 30, 59–64, 68–9; pl. 7, figs 1–3
Tomidaster sulcatus 200
tourtiae, Glenotremites 224
transversus, Holaster 142
tricarinata, Labrotaxis 15, 17, 23–5, 30, 161–6; pl. 32, figs 1–4; pl. 33, fig. 3
trigonalis, Epiaster 173
trigonopygus, Caratomus 115
trigonopygus, Echinogalerus 115, 119
truncatus, Cardiaster 16–17, 23–5, 166–7; pl. 19, figs 5–7
tumidus, Epiaster 173
Tylasteria 205
Tylocidaris 20, 40–3
  clavigera 43
  velifera 15, 17, 20, 25, 40–3; pl. 2, figs 1–2, 4–5
Typocidaris essenensis 37

umbrella, Hyposalenia 15–17, 25, 28, 35, 53–5; pl. 5, figs 1–3
undulatus sp. nov., *Isocrinus*(?) 15, 216–21; pls 45, 46; pl. 47, figs 2, 4; pl. 48, figs 1–2, 4
uniformis, Stereocidaris 37–40; pl. 1, figs 1–3; pl. 2, figs 7–8
Urechinus 23

Valettaster 194
  argus 195
  ocellatus 194–5; pl. 41, fig. 1
valettei, Glenotremites 224
Valvatida 193
variolare, Tetragramma 15, 17, 20, 25, 28, 69–74; pl. 9, figs 1–4
velifera, Tylocidaris 15, 17, 20, 25, 40–3; pl. 2, figs 1–2, 4–5
vesiculosa, Cidaris 37, 40
villersensis, Mastaster 189, 203–4; pl. 42, figs 3–7; pl. 43, fig. 3

wrighti, Mastaster villersensis 205

Zeugopleuridae 83

Typeset by Santype International Limited, Salisbury, Wiltshire
Printed in Great Britain at the University Printing House, Oxford

Accepted for publication 19 February 1986

Bulletin of the British Museum (Natural History)

Geology Series

Most earlier Geology *Bulletins* are still in print. A full list of available titles can be obtained from Publications Sales (address inside front cover).

Vol. 29 No. 1	Aspects of mid-Cretaceous stratigraphical micropalaeontology. D. J. Carter & M. B. Hart. 1977. Pp. 1–135, 4 plates, 53 figs.	£14.25
Vol. 29 No. 2	The Macrosemiidae, a Mesozoic family of holostean fishes. A. W. H. Bartram. 1977. Pp. 137–234, 4 plates, 53 figs.	£10.00
Vol. 29 No. 3	The stratigraphy and ammonite fauna of the Upper Lias of Northamptonshire. M. K. Howarth. 1978. Pp. 235–288, 9 plates, 5 figs.	£6.00
Vol. 29 No. 4	Fossil Bovidae (Mammalia) of Olduvai Gorge, Tanzania, Part I. A. W. Gentry & A. Gentry. 1978. Pp. 289–446, 41 plates, 34 figs.	£17.50
Vol. 30 No. 1	Fossil Bovidae (Mammalia) of Olduvai Gorge, Tanzania. Part II. A. W. Gentry & A. Gentry. 1978. Pp. 1–83, 3 figs.	£7.50
Vol. 30 No. 2	A revision of the Miocene Hominoidea of East Africa. P. J. Andrews. 1978. Pp. 85–224, 7 plates, 29 figs.	£15.30
Vol. 30 No. 3	Early Ordovician (Arenig) stratigraphy and faunas of the Carmarthen district, south-west Wales. R. A. Fortey & R. M. Owens. 1978. Pp. 225–296, 11 plates, 12 figs.	£9.60
Vol. 30 No. 4	Macroscopic inclusions of fluid in British fluorites from the mineral collection of the British Museum (Natural History). A. H. Rankin. 1978. Pp. 297–307, coloured frontispiece, 9 plates (7 coloured), 4 figs.	£12.00
Vol. 31 No. 1	Foraminifera of the Togopi Formation, eastern Sabah, Malaysia. J. E. Whittaker & R. L. Hodgkinson. 1979. Pp. 1–120, 10 plates, 71 figs.	£14.00
Vol. 31 No. 2	Cretaceous faunas from Zululand and Natal, South Africa. The ammonite family Gaudryceratidae. W. J. Kennedy & H. C. Klinger. 1979. Pp. 121–173.	£6.25
Vol. 31 No. 3	Benthic community organization in the Ludlow Series of the Welsh Borderland. R. Watkins. 1979. Pp. 175–279.	£12.25
Vol. 31 No. 4	The ammonites of the English Chalk Rock (Upper Turonian). C. W. Wright. 1979. Pp. 281–330.	£6.50
Vol. 32 No. 1	Miscellanea: Observations on *Cycloclypeus*—Provenance of *Sivapithecus*—Iranian Silurian brachiopods—New English condylarths—Miocene sharks' teeth—East African isopod—The Singa skull—Carboniferous insects. 1979. Pp. 1–90.	£10.50
Vol. 32 No. 2	Palaeoenvironments and correlations of the Carboniferous rocks in west Fermanagh, Ireland. C. H. C. Brunton & T. R. Mason. 1979. Pp. 91–108, 6 figs, folded map.	£4.00
Vol. 32 No. 3	The Ordovician trilobite faunas of the Builth–Llandrindod Inlier, central Wales. Part III. C. P. Hughes. 1979. Pp. 109–181, 177 figs.	£10.00
Vol. 32 No. 4	The stratigraphy and brachiopods of the upper part of the type Caradoc of south Salop. J. M. Hurst. 1979. Pp. 183–304, 557 figs.	£18.50
Vol. 33 No. 1	An account of the Ordovician rocks of the Shelve Inlier in west Salop and part of north Powys. W. F. Whittard, F. R. S. (Compiled by W. T. Dean). 1979. Pp. 1–69, 38 figs, frontispiece, coloured map, folded, in pocket. (Map available separately for £1.00)	£10.00
Vol. 33 No. 2	Miscellanea: Lower Carboniferous microproblematicum—Miniature trilobite—Pleistocene bird remains—English Eocene *Hyracotherium*—*Salenia trisuranalis*—Antarctic brachiopods—*Diphyphyllum* and Murchison's Russian corals—Lebanese amber Neuroptera. 1980. Pp. 71–164.	£12.00
Vol. 33 No. 3	The Caradoc faunal associations of the area between Bala and Dinas Mawddwy, north Wales. M. G. Lockley. 1980. Pp. 165–235, 105 figs.	£9.00
Vol. 33 No. 4	Fossil insects from the Bembridge Marls, Palaeogene of the Isle of Wight, southern England. E. A. Jarzembowski. 1980. Pp. 237–293, 77 figs.	£7.50
Vol. 33 No. 5	The Yorkshire Jurassic fern *Phlebopteris braunii* (Goeppert) and its reference to *Matonia* R.Br. T. M. Harris. 1980. Pp. 295–311, 20 figs.	£2.75
Vol. 34 No. 1	Relative dating of the fossil hominids of Europe. K. P. Oakley. 1980. Pp. 1–63, 6 figs, 17 tables.	£8.00
Vol. 34 No. 2	Origin, evolution and systematics of the dwarf Acanthoceratid *Protacanthoceras* Spath, 1923 (Cretaceous Ammonoidea). C. W. Wright & W. J. Kennedy. 1980. Pp. 65–107, 61 figs.	£6.25
Vol. 34 No. 3	Ashgill Brachiopoda from the Glyn Ceiriog District, north Wales. N. Hiller. 1980. Pp. 109–216, 408 figs.	£14.75
Vol. 34 No. 4	Miscellanea: Upper Palaeozoic Athyrididae brachiopods—New British Cretaceous Epitoniidae—Microproblematicum *Prethocoprolithus*—Glabellar structure of asaphid trilobites—New Lower Ordovician bivalve family—Cretaceous brachiopods—*Tupus diluculum* sp. nov.—Revision of *Plummerita*. 1980. Pp. 217–297.	£11.00
Vol. 35 No. 1	Lower Ordovician Brachiopoda from mid and south-west Wales. M. G. Lockley & A. Williams. 1981. Pp. 1–78, 263 figs, 3 tables.	£10.80
Vol. 35 No. 2	The fossil alga *Girvanella* Nicholson & Etheridge. H. M. C. Danielli. 1981. Pp. 79–107, 8 figs, 3 tables.	£4.20

Vol. 35 No. 3 Centenary Miscellanea: Budleigh Salterton brachiopods—Oswald's Turkish algae—J. A. Moy-Thomas—Burials, bodies and beheadings—*Nucleolites clunicularis*—*Phanerotinus cristatus*—Fossil record of teleosts—Neanderthal dating—*Hippoporidra edax*. 1981. Pp. 109–252.	£20.00
Vol. 35 No. 4 The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the Plesiosauria. D. S. Brown. 1981. Pp. 253–347, 44 figs.	£13.00
Vol. 36 No. 1 Middle Cambrian trilobites from the Sosink Formation, Derik–Mardin district, south-eastern Turkey. W. T. Dean. 1982. Pp. 1–41, 68 figs.	£5.80
Vol. 36 No. 2 Miscellanea: Dinantian terebratulids—New microfossils—*Neseuretus*—*Archaeocidaris whatleyensis*—Carboniferous dasyclad—*Nanjinoporella*—Toarcian bryozoans—Drybrook Sandstone plants—British fossil bintoniellids—*Uraloporella*. 1982. Pp. 43–155.	£19.80
Vol. 36 No. 3 The Ordovician Graptolites of Spitsbergen. R. A. Cooper & R. A. Fortey. 1982. Pp. 157–302, 6 plates, 83 figs, 2 tables.	£20.50
Vol. 36 No. 4 Campanian and Maastrichtian sphenodiscid ammonites from southern Nigeria. P. M. P. Zaborski. 1982. Pp. 303–332, 36 figs.	£4.00
Vol. 37 No. 1 Taxonomy of the arthrodire *Phlyctaenius* from the Lower or Middle Devonian of Campbellton, New Brunswick, Canada. V. T. Young. 1983. Pp. 1–35, 18 figs.	£5.00
Vol. 37 No. 2 *Ailsacrinus* gen. nov., an aberrant millericrinid from the Middle Jurassic of Britain. P. D. Taylor. 1983. Pp. 37–77, 48 figs, 1 table.	£5.90
Vol. 37 No. 3 Miscellanea: Permian *Glossopteris* in Turkey—Wealden *Theriosuchus*—Wealden conifer—Permian plants of Saudi Arabia—Carboniferous Edrioasteroidea—British cicadas—Dittonian cephalaspids. 1983. Pp. 79–171.	£13.50
Vol. 37 No. 4 The relationships of the palaeoniscid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia. B. G. Gardiner. 1984. Pp. 173–428, 145 figs, 4 plates. 0 565 00967 2.	£39.00
Vol. 38 No. 1 New tertiary pycnodonts from the Tilemsi valley, Republic of Mali. A. E. Longbottom. 1984. Pp. 1–26, 29 figs, 3 tables. 0 565 07000 2.	£3.90
Vol. 38 No. 2 Silicified brachiopods from the Viséan of County Fermanagh, Ireland. (III) Rhynchonellids, Spiriferids and Terebratulids. C. H. C. Brunton. 1984. Pp. 27–130, 213 figs. 0 565 07001 0.	£16.20
Vol. 38 No. 3 The Llandovery Series of the Type Area. L. R. M. Cocks, N. H. Woodcock, R. B. Rickards, J. T. Temple & P. D. Lane. 1984. Pp. 131–182, 70 figs. 0 565 07004 5.	£7.80
Vol. 38 No. 4 Lower Ordovician Brachiopoda from the Tourmakeady Limestone, Co. Mayo, Ireland. A. Williams & G. B. Curry. 1985. Pp. 183–269, 214 figs. 0 565 07003 7.	£14.50
Vol. 38 No. 5 Miscellanea: Productacean growth and shell shape—Jurassic alga *Palaeosiphonium*—Upper Ordovician brachiopods and trilobites—Lower Devonian Osteostraci from Podolia—*Hipparion* from Diavata—Preparation and study of Singa skull—Carboniferous and Permian bryozoa—Lower Eocene trionychid—Montsech fossil insects. 1985. Pp. 271–412. 0 565 07004 5.	£24.00
Vol. 39 No. 1 Upper Cretaceous ammonites from the Calabar region, south-east Nigeria. P. M. P. Zaborski. 1985. Pp. 1–72, 66 figs. 0 565 07006 1.	£11.00
Vol. 39 No. 2 Cenomanian and Turonian ammonites from the Novo Redondo area, Angola. M. K. Howarth. 1985. Pp. 73–105. 33 figs. 0 565 07006 1.	£5.60
Vol. 39 No. 3 The systematics and palaeogeography of the Lower Jurassic insects of Dorset, England. P. E. S. Whalley. 1985. Pp. 107–189, 87 figs, 2 tables. 0 565 07008 8.	£14.00
Vol. 39 No. 4 Mammals from the Bartonian (middle/late Eocene) of the Hampshire Basin, southern England. J. J. Hooker. 1986. Pp. 191–478, 71 figs, 39 tables. 0 565 07009 6.	£49.50
Vol. 40 No. 1 The Ordovician graptolites of the Shelve District, Shropshire. I. Strachan. 1986. Pp. 1–58, 38 figs. 0 565 07010 X.	£9.00
Vol. 40 No. 2 The Cretaceous echinoid *Boletechinus*, with notes on the phylogeny of the Glyphocyphidae and Temnopleuridae. D. N. Lewis. 1986. Pp. 59–90, 11 figs, 7 tables. 0 565 07011 8.	£5.60
Vol. 40 No. 3 The trilobite fauna of the Raheen Formation (upper Caradoc), Co. Waterford, Ireland. A. W. Owen, R. P. Tripp & S. F. Morris. 1986. Pp. 91–122, 88 figs. 0 565 07012 6.	£5.60
Vol. 40 No. 4 Miscellanea I: Lower Turonian cirripede—Indian coleoid *Naefia*—Cretaceous–Recent Craniidae—Lectotypes of Girvan trilobites—Brachiopods from Provence—Lower Cretaceous cheilostomes. 1986. Pp. 125–222. 0 565 07013 4.	£19.00
Vol. 40 No. 5 Miscellanea II: New material of *Kimmerosaurus*—Edgehills Sandstone plants—Lithogeochemistry of Mendip rocks—Specimens previously recorded as teuthids—Carboniferous lycopsid *Anabathra*—*Meyenodendron*, new Alaskan lepidodendrid. 1986. Pp. 225–297. 0 565 07014 2.	£13.00
Vol. 41 No. 1 The Downtonian ostracoderm *Sclerodus* Agassiz (Osteostraci: Tremataspididae). P. L. Forey. 1987. Pp. 1–30. 11 figs. 0 565 07015 0.	£5.50
Vol. 41 No. 2 Lower Turonian (Cretaceous) ammonites from south-east Nigeria. P. M. P. Zaborski. 1987. Pp. 31–66. 46 figs. 0 565 07016 9.	£6.50
Vol. 41 No. 3 The Arenig Series in South Wales: Stratigraphy and Palaeontology. I. The Arenig Series in South Wales. R. A. Fortey & R. M. Owens. II. Appendix. Acritarchs and Chitinozoa from the Arenig Series of South-west Wales. S. G. Molyneux. 1987. Pp. 67–364. 289 figs. 0 565 07017 7.	£59.00
Vol. 41 No. 4 Miocene geology and palaeontology of Ad Dabtiyah, Saudi Arabia. Compiled by P. J. Whybrow. 1987. Pp. 365–457, 54 figs. 0 565 07019 3.	£18.00
Vol. 42 complete Cenomanian and Lower Turonian echinoderms from Wilmington, south-east Devon. A. B. Smith, C. R. C. Paul, A. S. Gale & S. K. Donovan. 1988. Pp. 1–245. figs, 51 Pls. 0 565 07018 5.	£46.50